Individual variation in sociality and social foraging strategies in the Australasian gannet (*Morus serrator)*

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Abstract

Animals in groups experience both costs and benefits from social associations. For instance, sociality may increase competition and the risk of disease exposure, while conversely providing benefits of increased predator protection, foraging efficiency and access to sources of social information. Colonial species live in a particularly complex social environment, presenting significant opportunity for intraspecific social interactions. Indeed access to social information, particularly in terms of social foraging, has frequently been proposed as an important factor driving coloniality. Both colonial breeding and foraging aggregations are characteristic traits among seabird species, making them an ideal system to study aspects of social foraging in relation to colonial living. However, due to the vast size of many seabird colonies and the long distance covered during foraging, it has previously been difficult to examine the scale of such foraging aggregations, and the individual factors that drive social behaviours. By simultaneously tracking 85% of the breeding population of a colony of Australasian gannets (*Morus serrator*), this thesis aims to quantify the importance of sociality across multiple contexts associated with foraging. I demonstrate that individuals associate at the colony at a frequency greater than expected by chance, and that this coordination at the colony provides foraging information, as co-departing individuals share more similar initial foraging locations. Using multi-layer social network analysis, I further demonstrate that individuals vary consistently in their sociality across foraging states (colony departure, commuting, foraging and colony return), but show individual flexibility in their social associations. This work also highlights the context-dependent nature of social foraging decisions, as the use of social foraging behaviour differed with habitat choice. Lastly, I examine social foraging decisions during commuting (following) and foraging (patch joining) in the context of a producer-scrounger foraging game. I provide evidence that use of exploitative foraging strategies varies with time and space during foraging, which are expected to relate to foraging motivation and scrounging opportunity. Overall, this thesis makes the first individual level quantification of social associations during foraging in a colonial seabird, highlighting both its importance to this population and its opportunistic nature.

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Chapter 1
General Introduction

Foraging in groups

Animals expend a significant portion of their energy budget locating, acquiring and processing food resources while foraging (Stephens *et al.* 2007). Thus individuals are expected to develop foraging strategies which maximise resource intake and minimise time and effort spent foraging (Stephens *et al.* 2007). However for animals in groups, the outcomes of foraging become dependent not only on the individual but are also interdependently linked to the foraging decisions and outcomes of others (Giraldeau & Caraco 2000). Foraging within a group exposes individuals to increased risk of competition, kleptoparistism and aggressive interactions (Giraldeau & Caraco 2000; Beauchamp 2014b; Ward & Webster 2016a). On the other hand, individuals within a group can also directly benefit from increased foraging efficiency, which can result from decreased search time, improved capture rate, or by gaining access to prey unavailable to a single forager (Giraldeau & Caraco 2000; Beauchamp 2014b; Ward & Webster 2016a). Thus for group foraging to evolve, it is expected that at the individual level, the increased costs of group participation will be overcome by the benefits gained (Ward & Webster 2016b). As such, social foraging theory concludes that group foraging strategies are likely to be most prevalent when the costs of competition are limited, as is seen when resources are unable to be monopolised and when food patches are temporary in nature, as joining individuals are also able to benefit from access to the resource (Beauchamp 2014b). In general, studies have found that as predicted, group foraging strategies are employed more often in unpredictable and patchy environments (Pöysä 1992; Johnson *et al.* 2002; Rafacz & Templeton 2003), and therefore it is important to understand the use of social foraging behaviours in species predominantly relying on these types of environments.

Although the circumstances favouring the evolution of social foraging strategies have occurred in a broad range of taxa, the benefits gained from social behaviours may not be evenly distributed among groups or individuals (Krause *et al.* 2015). Within a group, individuals may experience different costs and benefits from social behaviours based on their intrinsic traits, including sex, age,

personality, competitive ability and foraging skill (i.e. Beauchamp 2006; Aplin & Morand-Ferron 2017). Similarly, individual motivation for engaging in social foraging will vary temporally in response to variation in previous foraging success and energetic reserves (Barta & Giraldeau 2000; Lendvai *et al.* 2004). Indeed, it has been proposed that variation between individuals is critical for the evolution of cooperative behaviours, including group foraging (Barta 2016). Therefore, in the study of social behaviours, it is critical to consider the individual level variation present within social groups, and it has been shown that understanding individual level variation can be critical in the understanding of population level processes (Réale *et al.* 2007; Taborsky & Oliveira 2012; Delgado *et al.* 2018; Gil *et al.* 2018; Webber & Vander Wal 2018).

One approach that has begun to address these between individual differences driving variation in social tendencies is the use of social network analysis. Social network methods aim to study social associations and social processes across individual, dyadic, group and even population levels, within a single common framework (Croft *et al.* 2008; Wey *et al.* 2008; Farine & Whitehead 2015; Krause *et al.* 2015). Recent developments in ecological uses of social networks have provided the necessary statistical methodology to address the non-independence inherent in social data and enable hypothesis testing through null model comparisons (Farine & Whitehead 2015; Farine 2017; Finn *et al.* 2019). Thus, social network methodologies provide a valuable statistical tool in which to address questions related to individual-level variation in sociality as well as social processes like the transmission of social information within a group.

Social foraging information

In addition to benefits gain from coordination of effort, foraging in social groups or in the presences of conspecifics and/or heterospecifics can allow individuals to use social information to influence their own foraging decisions. This information is acquired through the observation of, or interaction with other individuals (Galef & Giraldeau 2001; Hoppitt & Laland 2013), to gain and maintain

information about the environment (Dall et al. 2005; Giraldeau & Dubois 2008). Social information can be gained through a variety of mechanisms, for instance, attraction to a specific task or location, public information and eavesdropping (Valone 1989, 2007; Danchin *et al.* 2004; Laland 2004; Bonnie & Earley 2007). Eavesdropping is when non-target individuals attend to signals exchanged between two or more other individuals, and is typically used to assess the competitive rankings of others (Bonnie & Earley 2007; Valone 2007). In the context of foraging, attraction to a specific task or location is often termed stimulus or local enhancement (Hoppitt & Laland 2013) and allows individuals to learn about novel locations or methods of foraging (Laland 2004). Public information is the term used to define information gathered from unintentional cues displayed by others which provide information about the quality of a patch (Valone 1989; Danchin *et al.* 2004). Using these types of socially acquired information allows individuals to exploit the foraging efforts of others to acquire less energetically expensive information, although this information is generally found to be of lower quality or accuracy than can be obtained through personal sampling of the environment (Giraldeau *et al.* 2002; Kendal *et al.* 2005; Galef 2009). In particular as the distance in space and/or time between the social cue and an individual's response to the social information increases, the reliability of the cue will decrease (Seppänen *et al.* 2007). Previous work has demonstrated that the choice between personal and social information sources depends on a variety of factors. For instance, it has been shown that individuals favour social information when the costs of obtaining personal information are particularly high (Laland 2004; Galef 2009). The distribution of resources in the environment has also been found to influence individual information gathering. Social information has been demonstrated to be of higher value when resources are unpredictable but clumped within the environment (Barta & Szép 1992; Rafacz & Templeton 2003), and as resources cues become more cryptic (Barta & Giraldeau 2001; Barrette & Giraldeau 2006). Therefore, to understand individual decisions regarding the use of social *vs.* personal information, it is important to consider how environmental factors influence the value of different information sources. Specifically, it may be of considerable importance to investigate social processes, like information

transmission, when studying species with highly variable environments and those experiencing significant climatic changes.

Exploitation of social foraging information

Understanding the foraging decisions of individuals requires an understanding of the costs and benefits faced by each individual. When individuals acquire foraging information socially through the observation of others this can be considered an exploitative foraging strategy, in which individuals are expected to gain foraging information at low cost to themselves (Giraldeau & Dubois 2008; Beauchamp 2014a). Frequently, exploitative social foraging strategies have been modelling using a game theoretic approach, as the expression of exploitative strategies in a population will be frequency dependent and thus are expected to exist at an evolutionarily stable state (Maynard Smith 1982). One model of exploitative foraging is the information sharing (IS) model. Under this model, individuals within a group are assumed to simultaneously both search for foraging opportunities and monitor other individuals, with a stable solution of joining all possible foraging opportunities (Clark & Mangel 1984). However this model's predictions lead to higher levels of joining than have generally been empirically observed and suggest that joining frequency should be fixed across time (Giraldeau & Beauchamp 1999). Alternatively, under the producer-scrounger (PS) model, individuals can play either the producing strategy, in which they search the environment for new foraging opportunities, or they can play scrounger, in which they search for opportunities to join other foragers (Barnard & Sibly 1981). In the initial PS model, individuals can engage in only one strategy at any given time point, but can sequentially switch between strategies over time, as the success of scrounging individuals decreases when they are more abundant (Giraldeau & Beauchamp 1999). An extension of the PS model demonstrates that depending on the level of incompatibility between the two strategies it is also possible for the existence of an opportunistic strategy which can search for both producing and scrounging opportunities simultaneously at reduced efficiency (Vickery et al. 1991). The existence of exploitative foraging strategies has been documented in a

variety of social systems, but has been particularly well studied in passerine birds, particularly small ground foraging species (i.e. Barnard & Sibly 1981; Koops & Giraldeau 1996; Beauchamp 2001; Flynn & Giraldeau 2001; Lendvai *et al.* 2006; Morand-Ferron *et al.* 2007; David *et al.* 2011). However, in any social system in which individuals can benefit from the foraging effort of others it is predicted that exploitative foraging strategies will evolve (Vickery *et al.* 1991), yet to date there has been limited work aiming to extend the concepts and models developed under the study of passerine foraging to other social systems.

Sociality in colonies

An individual's access to, and ability to employ social foraging tactics is dependent on the surrounding social environment. Therefore, the use and benefits of social foraging strategies will be strongly influenced by group size and structure (Clark & Mangel 1986; King & Cowlishaw 2007; Cvikel *et al.* 2015). Coloniality is specific form of group living, in which individuals occur in dense aggregations at sites with no defendable resources during breeding or roosting, at densities much higher than expected by ideal free distribution (see reviews by Danchin and Wagner 1997; Evans et al. 2016). While colonial living is prevalent in a range of taxa, there remains a lack of consensus in the understanding of the evolution of colonies (Danchin & Wagner 1997; Rolland *et al.* 1998). Given the high costs expected to result from living in dense groups, such as resource competition, disease and parasite transmission and cuckoldry, it has been proposed that enhanced access to social information may be a significant driving factor in the formation and maintenance of colonies (Evans *et al.* 2016). In particular it has been suggested that socially facilitated foraging may be a key benefit to many colonially breeding and roosting birds (Ward and Zahavi 1973; Clode 1993; Bijleveld et al. 2010; Evans et al. 2016). However, while there has been considerable interest in understanding the role of social information in the evolution and maintenance of colonies, it remains difficult to study social processes at the necessary individual level due to the size of many colonies and the difficult

nature of observing social associations that often occur infrequently and in inaccessible locations (Krause *et al.* 2013).

Even among colonial species, the role of the colony is thought to be particularly important for colonial breeders that make repeated foraging trips to provision offspring starting and ending at a fixed location (the colony). In this case, there is significant opportunity for the colony can act as a central point for information transmission (information centre hypothesis; Ward and Zahavi 1973; recruitment centre hypothesis; Richner and Heeb 1995). Under the initial hypothesis, Ward and Zahavi (1973) present that communal roosts and breeding colonies act as a place for information transmission, with previously unsuccessful foragers following other more successful individuals from the colony location to foraging sites. However, considerable debate exists about the requirements of the initial hypothesis, which indicates that individuals must actively advertise their success in order to be followed by previously unsuccessful individuals, and thus has been suggested to require some form of reciprocal altruism in order to function (Mock et al. 1988; Richner & Heeb 1995; Danchin & Richner 2001). In an alternative model, the recruitment centre hypothesis, the authors present that if individuals benefit from group foraging, for instance through increased foraging efficiency over solitary foraging, only then should individuals return to the colony to actively recruit other foragers (Richner & Heeb 1995). Despite the number of studies that have considered these hypothesis, little attention has been given to the potential for inadvertent, rather than active, sharing of information at colony sites (reviewed in Evans et al. 2016). When it is not possible to conceal information, the production of potentially exploitable social information is unavoidable (Danchin et al. 2004). Thus, the colony may act as a source of information transmission without intentional information transfer, and this unintentional information transmission at the colony can be effectively modelled as a PS model in which scroungers at the colony look for opportunities to follow departing foragers (Barta & Giraldeau 2001).

Congregation of individuals at a fixed central location also concentrates foragers in the accessible foraging grounds near the colony, where the highest resource depletion will occur (Ashmole 1963; Buckley 1997). This congregation of foraging individuals also allows for the transmission of foraging information away from the colony. For instance, local enhancement, in which an individual obtains social information due to the foraging behaviour of other individuals (Pöysä 1992) occurs at the location of the resource. In some cases, foraging individuals may actively recruit others to join a foraging patch through deliberate signals (e.g. cliff swallows (*Hirundo pyrrhonota)* emit foraging calls to attract conspecifics; Brown et al. 1991) particularly if foraging is more efficient in groups. However, often local enhancement will occur passively due to the production of unintentional cues (Galef & Giraldeau 2001). Local enhancement has also been shown to be particularly important in patchy environments (Pöysä 1992) and models have indicated that as resources become more clumped and patchy both local enhancement and information centre forms of transmission are favoured over individual searching (Barta & Szép 1992). In addition to acquiring information about when and where to feed (local enhancement), individuals may also attend to the foraging success and patch departure decisions of others to obtain public information about the quality of and/or depletion of a resource (Dall et al. 2005; Hoppitt & Laland 2013). For colonial breeders, matching a patch departure to other individuals returning to the same colony may also provide opportunities for reduced travel costs (Weimerskirch et al. 2001; Portugal et al. 2014) and increased navigational ability (Codling & Bode 2016). Although it has been demonstrated that local enhancement and public information should be highly available to colonial species, there is still little known about how individuals vary in their use of these information sources and how these decisions are influenced by both internal and external factors. Due to the complex social environment of colonial animals, these species make and excellent model system in which to address these outstanding questions about individual forging decisions and social foraging behaviours in general.

Social foraging in seabirds

Colonial breeding is extremely prevalent in seabirds, with approximately 95% of the 350 or so seabird species breeding in some form of colony (Coulson 2001). Seabird colonies are variable in size, but can often range from hundreds to thousands of individuals, exerting considerable predation pressure on the surrounding environment (Ashmole 1963; de L. Brooke 2004). Additionally, the marine environment in which seabirds forage presents highly spatially and temporally variable resource patches (Weimerskirch 2007), which is expected to further promote the use of social foraging behaviours (Barta & Szép 1992; Galef 2009). During the breeding season at least, seabirds engage in central place foraging, in which individuals must frequently return to the colony to provision their offspring, and thus individuals are restricted in the foraging areas they can access. These characteristics make seabirds a particularly appealing model in which to investigate existing questions about social foraging, and social information use in particular.

The potential importance of sociality in seabirds has been highlighted through an individual based model constructed to model seabird foraging behaviours. This model has demonstrated that the use of both information centre type information and local enhancement can reduce both foraging trip time and failure rate when prey is spatially clumped (Boyd et al. 2016), emphasising the potential benefits individuals may receive from the use of social foraging behaviours. Due to the large spatial scale at which seabirds forage, there has been limited direct evidence to confirm these suggestions or to address the importance of social foraging and information use in seabirds. However, the increasing use of bio-logging technology (i.e. cameras and GPS) has allowed researchers to now track individuals in fine-scale detail during foraging trips at-sea (Yoda 2019). These technologies mean it is now possible to begin to address the individual level social decisions made by colonial foraging seabirds, and the intrinsic and extrinsic factors influencing these decisions.

Although there has been considerable interest in the hypothesis that colonies may act as a source of information, previous work in seabirds has mostly inferred social information use from colony level data or been limited to observations of individuals departing the colony with mixed findings. For instance, a large-scale study of neighbouring colonies of northern gannets (*Morus bassanus)* demonstrated that colonies showed little overlap with each other, providing evidence that within colony public social information may drive segregation between foraging areas of different colonies (Wakefield *et al.* 2013). However, such colony level segregation has been found to differ between species, with large between-colony overlap detected in colonies of European shags (*Phalacrocorax aristotelis)* (Evans *et al.* 2015). Additionally, previous work showing that seabirds match their departure directions to the direction of other departing and/or incoming birds, proposes that information may be obtained at the colony or at rafts of birds that form on the water near the colony (Weimerskirch *et al.* 2010; Machovsky-Capuska *et al.* 2013; Waggitt *et al.* 2014; Goyert 2015; Carter *et al.* 2016). Conversely, a tracking study conducted in a large colony of ring-billed gulls (*Larus delawarensis*) demonstrated that while reliable foraging information was available from the departure headings of individuals, birds did not match their departure direction with that of colony-mates (Racine et al. 2012). This current evidence highlights that information is likely to be available at the colony site, but it is still unclear to what extent individuals make use of such information. Particularly, given the context-dependent value of social information, it is important to investigate how different populations and individuals within a population may use social information differently depending on the environmental features of the habitats in which they forage.

Critically, to assess if information is being acquired at or near the colony from the observation or interaction with other individuals, it is important to assess the effects of this information on foraging decisions. Bird-borne cameras have demonstrated that individuals respond to the presence of foraging individuals and the direction of flying individuals, by altering their own flight heading (Votier *et al.* 2013; Thiebault *et al.* 2014b; Tremblay *et al.* 2014). Furthermore, when individuals responded to direction of incoming birds, they were shown to reach foraging patches sooner (Thiebault et al.

2014b). While bird-borne cameras provide unique information on at-sea social interactions they have a limited time range (often recording only the initial portion of a foraging trip) and are generally only deployable on a small number of individuals at one time, thus providing only a partial picture of the social foraging behaviours of seabirds. There is still limited evidence assessing if the colony site acts as a centre for information transmission in colonially breeding seabirds, although recent GPS data from Socotra cormorants (*Phalacrocorax nigrogularis*), has demonstrated on a small sample that individuals departing the colony close in time did forage over the same foraging grounds (Cook *et al.* 2017).

Additionally, as the breeding colony presents a fixed point of aggregation, the colony may provide an efficient location for group formation prior to the initiation of foraging trips, which could facilitate group foraging at the patch site. This has been observed in little penguins (*Eudyptula minor*) that associate during colony departures as well as perform synchronized dives at sea (Daniel et al. 2007; Berlincourt & Arnould 2014). Forming foraging groups at the colony could enable individuals to reduce their search time through group search effort (Beauchamp 2014a). It could also allow individuals to scrounge foraging information from other individuals by following departing individuals to foraging patches (Barta & Giraldeau 2001). For instance, following behaviour has been observed in colonial roosting Eurasian griffon vultures (*Gyps fulvus*), in which uninformed individuals were found to follow informed vultures to locate foraging patches (Harel *et al.* 2017). Similarly, a recent study of northern gannets demonstrated that juvenile individuals, who are expected to have less foraging experience, were found to be more likely to follow during group flights (Wakefield *et al.* 2019). Although, there may also be energy saving benefits during flight to following behaviour (Weimerskirch *et al.* 2001; Portugal *et al.* 2014), this study observed no significant difference in flight abilities between adults and juveniles, highlighting the potential information benefit to following (Wakefield *et al.* 2019). It has also been demonstrated that information transfer in travelling groups can occur even when individuals are unaware which individuals in the group are 'informed' (Couzin *et al.* 2005).

In addition to at-colony behaviours, it has long been observed that seabirds aggregate while foraging at sea, and it has been suggested that these foraging aggregations provide a cue of foraging information (Coulson 2001). GPS tracking data has now demonstrated in several seabird species that individuals overlap at foraging locations (Daniel *et al.* 2007; Berlincourt & Arnould 2014; Cook *et al.* 2017; Sutton *et al.* 2017; Brisson-Curadeau *et al.* 2018). Furthermore, experimentally placed decoy birds have been shown to attract both conspecific and heterospecific seabirds, particularly during periods of low prey predictability (Bairos-Novak et al. 2015), highlighting the use of local enhancement strategies in colonial seabirds. However, current studies have been unable to quantify how individuals may vary their reliance on local enhancement in relation to temporal and spatial factors.

Several studies of group foraging behaviours in seabirds have also provided evidence that group foraging may increase individual foraging efficiency. For instance in Cape gannets (*Morus capensis),* individual probability of prey capture was highest when a dive occurred within 1-15 seconds of another individual's dive (Thiebault *et al.* 2016). This study demonstrates that diving in this time-window corresponded to the period of maximum disruption to the fish school. In other species, conspecific and heterospecific group foraging has been shown to herd prey into a more easily exploited bait balls (Vaughn *et al.* 2010; Ryan *et al.* 2012). Furthermore, evidence of coordination of dive effort has been shown in several species. For instance in several species of penguins individuals have been found to synchronize dives with conspecific associates (Takahashi *et al.* 2004; Daniel *et al.* 2007; Berlincourt & Arnould 2014; McInnes *et al.* 2017), while in European shags, individuals dive in close succession to other diving individuals in their field of view (Evans *et al.* 2019).

Study system

Data for this thesis was collected through GPS tracking of breeding adult Australasian gannets *(Morus serrator*; hereafter gannet). Gannets are an ideal system in which to study social foraging

behaviours across foraging trips. Gannets are highly conspicuous colonial breeding seabirds that forage by plunge diving (Nelson 1978). Because birds typically gain information visually (Fernández-Juricic *et al.* 2004), and gannets specifically are known to rely on visual cues when locating foraging patches (Machovsky-Capuska *et al.* 2012), the highly visible white plumage of gannets coupled with their plunge dives can be expected to make foraging individuals an easily accessible foraging cue (Bretagnolle 1993; Weimerskirch *et al.* 2010). Furthermore, it has been shown that plunge diving is an extremely energetically expensive foraging method (Green *et al.* 2009), as such individuals should attempt to minimise their dive effort by only diving when there is high likelihood of obtaining prey. Thus, individual should be expected to gain as much information as possible before engaging in plunge dives. Finally, the large size of gannets enables the use of GPS devices that can record data of multiple trips per individual.

The colony studied was based at Pope's Eye, located in Port Phillip Bay, Australia (38°16'42"S, 144°41'48"E; Figure 1.1). This small colony of gannets was established in 1984 and is located on an artificial wooden platform, with birds nesting on available flat surfaces (Pyk *et al.* 2013). This colony consists of up to approximately 130 nests (Pyk *et al.* 2013), although at the time of data collection in 2015, the study site consisted of approximately 50 active nests (JPYA personal observation). This colony is thought to have formed from overflow of larger colonies located in Bass Strait (Bunce *et al.* 2002) although recent work suggests that the foraging areas of these colonies do not overlap (Angel *et al.* 2016).

The work in this thesis undertakes a novel assessment of social behaviours across multiple spatial and temporal foraging contexts in colonial seabirds, using recently developed social network methodologies and the most comprehensive colony-wide sampling to date. During this study 85% of the breeding adults were simultaneously tracked by GPS over multiple trips, during the chick-rearing period. The data used in this thesis was collected by collaborators from Deakin University during the 2015 breeding season to address questions related to social foraging, and as an extension of

previous studies monitoring this colony. The chick-rearing period has been shown to be a particularly energy intensive period for seabirds (Dunn et al 2018) including this population (Green *et al.* 2013; Dunn *et al.* 2018). Due to this high energetic demand, social associations may be of particular importance during this period. This data presents a novel high-resolution, near-complete colony look at individual social decisions across whole foraging trips that has previously not been possible in any colonial system, and enables this thesis to address a number of unanswered questions about seabird sociality and animal social foraging in general.

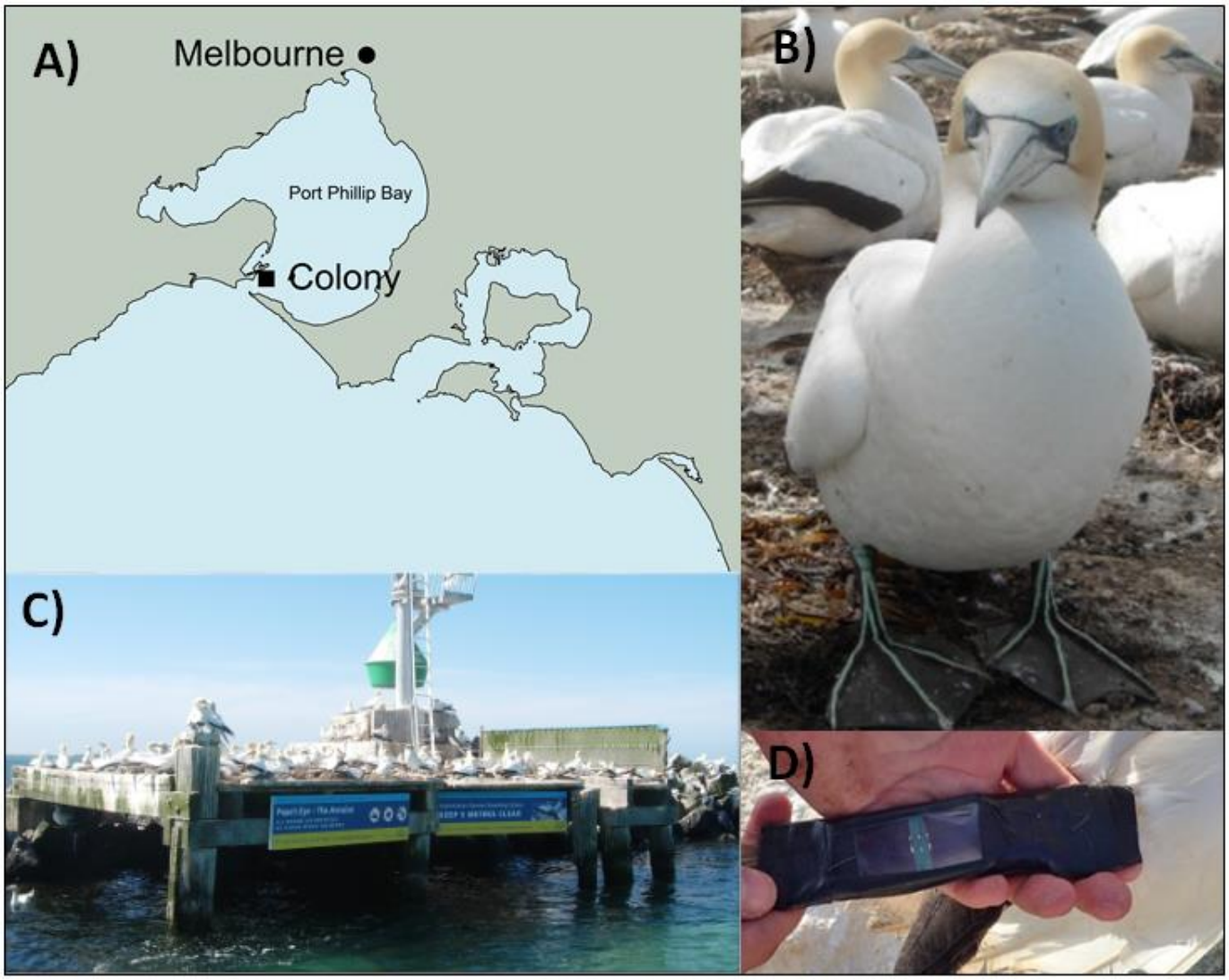

Figure 1.1 Thesis study system. A) Map of Pope's Eye colony located in Port Phillip Bay, Australia. B) Photo of an Australian gannet C) Photo of the nesting platform at Pope's eye colony. D) Photo of a GPS tag device fitted to the tail of a gannet.

Thesis outline

In this thesis I examine the extent and importance of social associations across multiple foraging contexts (colony departures, commuting flight, foraging and colony returns) of a small colony of Australasian gannets. Colony departures and returns reflect the initial and final direction of travel by individuals on foraging trips. Commuting flight are periods of the foraging trip in which individuals exhibit fast directed flight indicating travel between foraging patches. Foraging behaviour is exhibited by slower flight and higher turning angles indicating individuals are performing active searching behaviour and dives. I also assess individual variation in social behaviours in response to the intrinsic and extrinsic drivers of sociality.

Chapter 2 examines how social association at the colony site influences foraging decisions. Colony associations were measured as colony co-departure and co-departing gannets were found to share more similar initial foraging locations. This study builds on the idea that the colony site may act as an information centre for birds departing on foraging trips, providing evidence that associations formed at the colony provide foraging information and/or provide a centralised location for foraging group formation. This chapter is published in Biology Letters.

Chapter 3 initially defines and identifies social associations across four foraging contexts (colony departure, commuting, foraging and colony return). I then use a novel multilayer social network analysis method to investigate how individual social associations and social tendencies vary across the four foraging contexts, and across two habitats, which differ in terms of prey type and distribution. I find that individuals express consistent social tendency across the four foraging stages, but exhibit flexibility in their social associations, demonstrating the highly dynamic fission-fusion nature of this system. Furthermore, the results of this study highlight the importance of local enhancement at foraging patches, but only in habitats with small shoaling fish. This chapter has been peer reviewed at Ecology Letters and is currently in revision.

Chapter 4 builds on the social commuting and foraging associations classified in **Chapter 3** and assesses how individuals vary their use of exploitative foraging strategies. During commuting, individuals may follow behind another commuting individual, allowing them to scrounge information from the leading individual, while during foraging, individuals can either locate new foraging areas, or join another individual at an active foraging patch. The results of this study demonstrate that individuals plastically adjust their use of scrounging strategies across their foraging trips, in response to metrics that are expected to reflect both temporal changes in energy reserves (time through foraging trip, time since previous foraging event, time of day, length of forage) and scrounging opportunity (distance from the colony). This chapter is in preparation for submission to The American Naturalist.

Chapter 5 Summarises the content of this thesis and presents the findings of this work in the wider context of group foraging and social information use. I also present future directions to further the understanding of social foraging decisions in colonial breeding species.

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Chapter 2

Evidence of sociality in the timing and location of foraging in a colonial seabird

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The study was conceived by TBJ, SCP, JPYA and JAG. Data was collected by MARM, MRW and JPYA. TBJ analysed the data and wrote the manuscript with support by SCP, JAG, & JPYA.

Abstract

Social foraging behaviours, which range from cooperative hunting to local enhancement, can result in increased prey capture and access to information, which may significantly reduce time and energy costs of acquiring prey. In colonial species, it has been proposed that the colony itself may act as a site of social information transfer and group formation. However, conclusive evidence from empirical studies is lacking. In particular, most studies in colonial species have generally focussed on either behaviours at the colony or at foraging sites in isolation, and have failed to directly connect social associations at the colony to social foraging. In this study, we simultaneously tracked 85% of a population of Australasian gannets (*Morus serrator*), over multiple foraging trips, to study social associations at the colony and test whether these association influence the location of foraging sites. We found that gannets positively associate with conspecifics while departing from the colony and that co-departing gannets have more similar initial foraging patches than individuals that did not associate at the colony. These results provide strong evidence for the theory that the colony may provide a source of information that influences foraging location.

Introduction

Social foraging, when an animal's foraging behaviours, and the resulting costs and benefits, are interdependently linked with the foraging behaviours of others (Giraldeau & Caraco 2000), is expected to develop when the benefits of social foraging outweigh the costs, such as increased competition (Beauchamp 2014b). Social foragers may directly benefit through decreased search time, improved capture rate, access to otherwise unavailable prey, or access to information (reviewed by Giraldeau & Caraco 2000; Beauchamp 2014b). Additionally, individuals may indirectly benefit from coordinating travel during foraging, through reducing overall energy expenditure by lowering movement costs (i.e. birds flying in formation; Weimerskirch *et al.* 2001), or predator protection effects (Beauchamp 2014b). Social foraging benefits are predicted to be most prevalent when costs of individual foraging are high (Galef 2009), resource detectability is low (Barrette & Giraldeau 2006), or resources are variable but clumped within the environment (Barta & Szép 1992).

For colonial species, large breeding or roosting aggregations provide significant potential for social foraging opportunities. It has been proposed that colonies can act as a location for information transmission (Ward & Zahavi 1973) and that the ready availability of social information may be a driving force in the evolution and maintenance of coloniality (Evans *et al.* 2016). However, previous studies examining the potential transmission of information at colonies, through direct between-pair signalling (Machovsky-Capuska *et al.* 2013) and colony co-departures, have produced mixed results (e.g. Weimerskirch *et al.* 2010; Racine *et al.* 2012; Machovsky-Capuska *et al.* 2013; Carter *et al.* 2016) and generally focus on either behaviours at the colony or foraging site separately (but see Machovsky-Capuska *et al.* 2013; Cook *et al.* 2017; Sutton *et al.* 2017), and so the link between these behaviours remains unresolved. Notably, without knowledge of subsequent foraging locations and availability of additional social (i.e. local enhancement; Pöysä 1992) and asocial information sources (i.e. environmental conditions), studies at the colony alone cannot determine whether or how these interactions translate into foraging information.

In the present study, we simultaneously tracked 85% of the active breeders from a small colony of Australasian gannets (*Morus serrator;* hereafter gannets). Gannets, like many seabirds, are colonial, forage in patchy marine environments, and frequently aggregate with both conspecific and heterospecifics at-sea (Vaughn *et al.* 2010). Evidence suggests seabirds use local enhancement by responding to the presence of foraging individuals (e.g. Tremblay *et al.* 2014), which can lead to earlier arrival at foraging patches (Thiebault *et al.* 2014a). However, due to the size of most seabird colonies, previous studies have been limited to observing only a very small proportion of the colony, providing an incomplete picture of a colony's behaviours making it difficult to infer sociality. Here, by concurrently tracking a large proportion of a colony, we test whether gannets preferentially form groups when departing on foraging trips, testing the potential for the use of colony cues. We then evaluate whether this results in collective foraging by determining if initial foraging patches are more similar when birds depart together. Finally, to provide evidence for social foraging opportunities away from the colony site, we investigate the extent to which gannets overlap in their initial foraging patches and determine if co-foraging gannets share more similar departure times, thus examining the link between coordination at the colony and foraging at-sea.

Methods

We collected behavioural data from adult gannets breeding on a small man made structure in Port Phillip Bay, south-eastern Australia (38°16'42"S, 144°41'48"E). Gannets N = 100 were fitted with GPS data loggers (igotU GT-600*;* sampling interval = 2 mins; See Supplemental Material for full details). All complete trips, from 09/01/2015 - 22/01/2015 were analysed, as this period covers the highest proportion of the colony simultaneously tracked.

We defined colony departure as the first GPS fix in a trip to cross a 500 m buffer around the colony (within 500 m birds may raft, thus we consider co-departures from either colony or raft). To determine how individuals departed from the colony in relation to others in the colony, we used a 3-

minute sliding time window to identify individuals departing the colony together (See Supplemental Materials for sensitivity of co-departure time-windows).

We used Expectation-Maximization binary Clustering (EMbC; R package EMbC v2.0.0 Garriga *et al.* 2016) to identify foraging behaviours (behaviours classified: foraging, commuting and resting; see Supplemental Materials for full details). A minimum convex polygon was fitted around the initial foraging patch (defined as >3 consecutive GPS fixes classified as foraging, with bouts merged when separated by < 5 minutes of non-foraging; see Mendez *et al.* 2017) of each trip (*rgeos* v0.3-26; Bivand & Rundel 2017). We identified all foraging patches which co-occurred in time (60 second buffer) and space (*sp* package v.12-5; Pebesma & Bivand 2017).

To determine if overlap in colony departures and foraging patches could be generated by chance, we compared the observed pattern to null models produced through randomisations of the timing of departures and foraging patches (for full details see Supplemental Materials). To investigate if gannets that shared foraging patches had more similar colony departures, we calculated the difference in departure times (log transformed; to account for non-normality) between pairs of birds in all co-occurring first foraging patches, and used a two-sample *t*-test to compare pairs of birds in overlapping and non-overlapping foraging patches.

We calculated the straight line distance between centroids of the first foraging patches of each trip, for each individual and 1) birds on trips that co-departed the colony with the focal trip and 2) all trips in which individuals were not observed co-departing with the focal trip. We used pair-wise Kolmogorov–Smirnov tests to determine if the distribution of distances varied between each group. All statistical analysis was performed in R v.3.3.1 (R Core Team 2016). Unless otherwise indicated, data are presented as mean ± SE.

Results

We recorded 938 complete foraging trips (duration; 16.1 ± 0.7 hours), from 85 individuals (11.04 ± 0.6 trips per bird), representing 85% of the breeding birds at the time of the study. Gannets preferentially departed the colony with conspecifics (40.7% of trips, 10 000 permutations; $p = 0.0068$, Figure 2.1A) and co-occurring foraging bouts tended to overlap in foraging area more often than expected by chance (27.4% of co-occurring first foraging bouts overlapped in space; 1000 permutations, $p = 0.001$, Figure 2.1B)

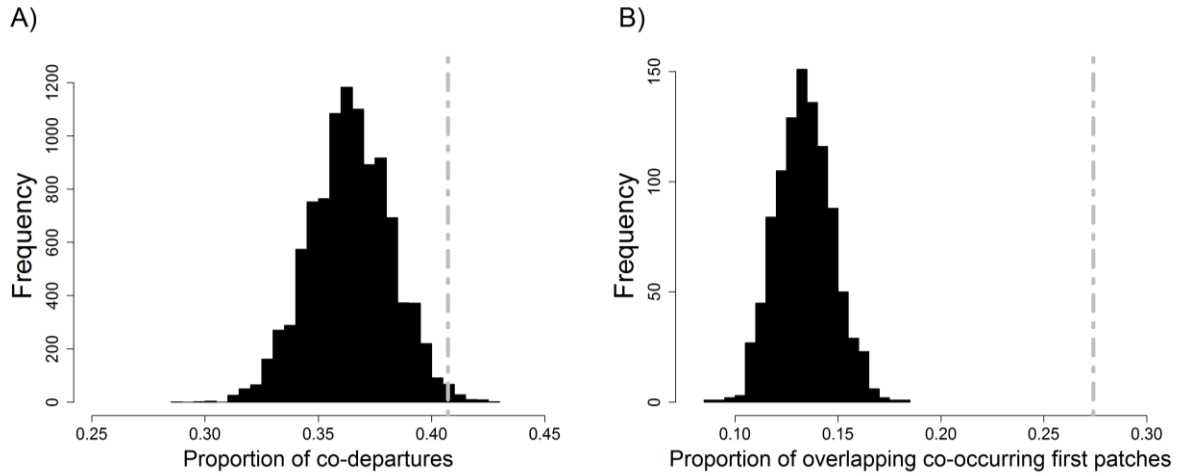


Figure 2.1 Distributions of temporal overlap for A) the proportion of trips in which at least one pair of individuals co-departed within a 3-minute time window and B) proportion of temporally co-occurring initial foraging patches that overlap in space, compared with the observed values (indicated by dashed line). Null model distributions for co-departures and patch overlap obtained from 10 000 and 1000 data permutations respectively.

Individuals with overlapping foraging patches had departures times that were 2.6 times closer than those with non-overlapping foraging patches (minutes apart: overlapping = 39 ± 4.9; non-overlapping = 100 ± 4.8; $t_{242} = -7.5$, $p < 0.0005$, Figure 2.2A). Co-departing individuals tended to have first foraging patches closer together than the first patches of birds that did not co-depart (k-s test; $D = 0.40$, $p < 0.0005$, Figure 2.2B).

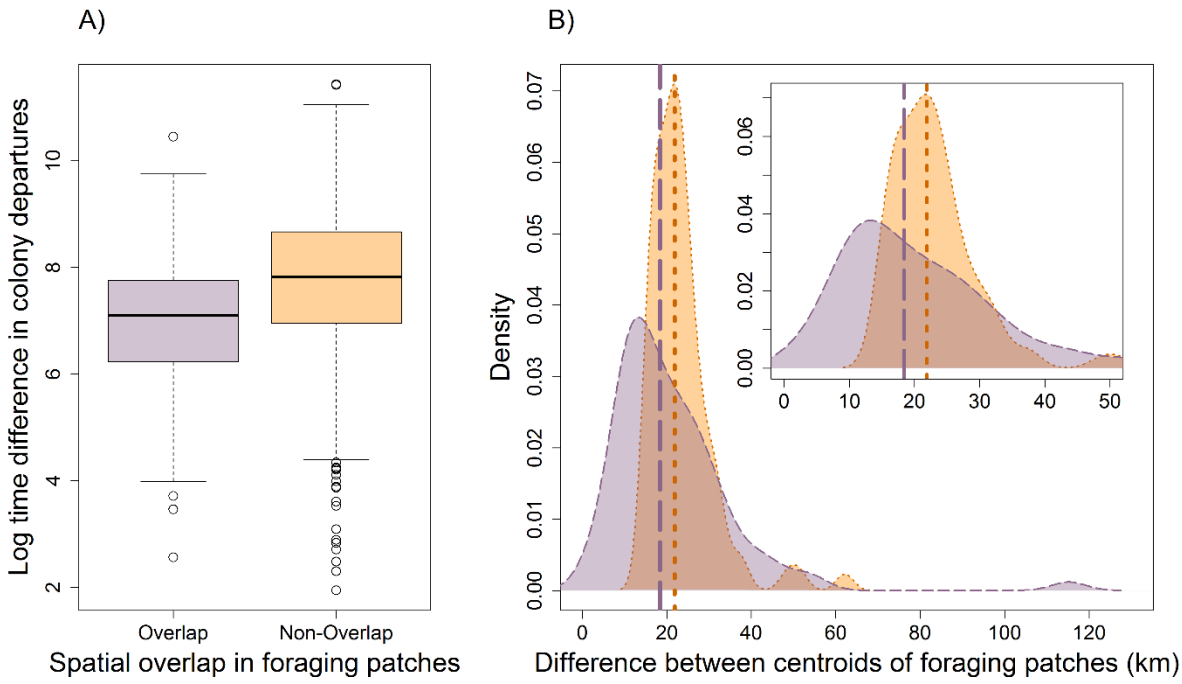


Figure 2.2 Similarity between first foraging patches and departure times of individuals. A) Log difference in colony departure times for gannets that share a first foraging patch (purple) and those which do not (orange) B) Average difference in distance (km) between central points of first foraging patches. Co-departing individuals are shown in dashed purple, and non co-departing pairs are shown in dotted orange. Insert shows 95% of data, for clarity. Lines indicate median values.

Discussion

In this study we used GPS to simultaneously track the foraging movements of 85% of the breeding adults in a colony of Australasian gannets and demonstrate that gannets coordinate foraging movements as part of their overall foraging strategy. Our results, which even with our comprehensive data set provide a conservative estimate of this coordination (Supplemental Material Fig 2), show individuals significantly overlap with conspecifics, during both colony departures and subsequently while foraging at-sea. Thus, our study presents robust colony-level support for the existence of social foraging behaviours in colonial seabirds.

As the colony is a central location to which breeding individuals must return, group formation at the colony may be beneficial to avoid locating foraging groups at-sea and/or foraging alone. Indeed, we found initial foraging patches were more similar for individuals that co-departed the colony,

indicating the colony may provide a site of group formation. Gannets travelling in groups may benefit through multiple mechanisms, including enhanced search ability, access to foraging information (Beauchamp 2014b), and reduced flight costs (Weimerskirch *et al.* 2001), factors that are difficult to disentangle, likely act in combination, and may all be considered aspects of social foraging. However, our data are spatio-temporal co-occurrences, and we did not directly observe inter-individual interactions or determine the effect of the external environment on individual decisions. Thus our conclusions rely on the assumption that concurrent foraging events represent interdependence in foraging outcomes (social foraging) (Giraldeau & Caraco 2000). Although it is impossible to completely disentangle this pattern from shared environmental drivers using remote tracking data, given the short time-scale over which we measure coordination, and the significant overlap observed beyond our null models we propose that the observed degree of co-occurrence is unlikely to be solely driven by shared external factors. Previous studies of social foraging in colonial seabirds rely on the same assumptions (e.g. Weimerskirch *et al.* 2010; Racine *et al.* 2012; Machovsky-Capuska *et al.* 2013; Cook *et al.* 2017), which are supported by direct observations of social foraging behaviours (Tremblay *et al.* 2014), that have been found to benefit individuals through reduce foraging time (Thiebault *et al.* 2014a) and increased prey capture (Thiebault *et al.* 2016).

As plunge-diving is a highly energetically expensive foraging mode (Green *et al.* 2009), gannets may attempt to minimise search time and unsuccessful dives by using conspecifics and heterospecifics cues. Previous work has highlighted how seabirds respond to aggregations at-sea, by joining experimental (Bairos-Novak *et al.* 2015) and natural foraging groups (Vaughn *et al.* 2010; Thiebault *et al.* 2014a; Tremblay *et al.* 2014). Social foraging can increase prey detection and capture in several species of seabirds through cooperative hunting. For instance, penguin species can cooperatively corral fish shoals (Ryan *et al.* 2012) and perform synchronised dives (e.g. Berlincourt & Arnould 2014), which may increase prey detection and/or capture as well as provide group protection through synchronisation. In Cape gannets (*M. capensis*) dive success increases two-fold when

occurring within seconds of a previous conspecific attack (Thiebault *et al.* 2016), and Australasian gannets exhibit high capture rate (72% success) in mixed-species aggregations (Machovsky Capuska *et al.* 2011). Our results demonstrate that individuals did share foraging areas as predicted, providing further evidence that conspecifics may provide social foraging benefits both at and away from the colony.

Our data simultaneously follows a large proportion of a colony providing evidence for social foraging behaviours of seabirds, allowing us to more completely capture colony-level social interactions. Although this evidence suggests that social overlap is significant and important across all stages of foraging trips (departure, prey location and foraging), further work modelling individual movements in conjunction with environmental data are necessary to disentangle the effects of social and shared abiotic factors which can both drive movement decisions. Similarly, future work quantifying the costs and benefits underlying social foraging, such as the energetic gains or losses during group and solitary foraging events are required to fully understand the consequences of social associations, and would further explain the role social foraging plays within the overall foraging strategy.

Supplementary Materials

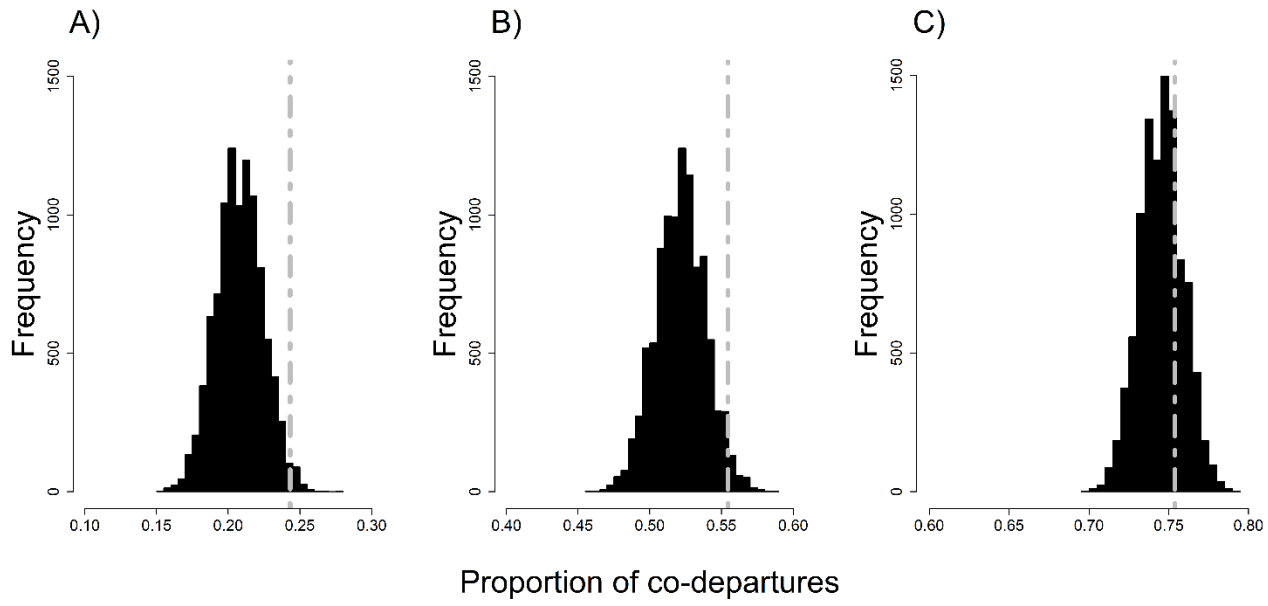
Data loggers and handling

Gannets were captured on their nests by hand and weighed in a cloth bag using a suspension scale (± 25 g, Salter). Each individual was then fitted with GPS data logger (igotU GT-600, Mobile Action, Taiwan, 26.6 g) packaged in heat shrink tubing and secured to the central tail feathers using water-proof tape (Tesa 4651, Beiersdorf AG, Germany), to minimise impact on aerodynamics during plunge diving (Ropert-Coudert *et al.* 2009). Individuals were then returned to the nest to resume normal behaviours with handling time lasting <6 min. Upon recaptures, devices were removed by peeling off the water-proof tape from the feathers, birds were again weighed and morphometric measurements were taken before release, with handling time lasting <15 min.

Colony departures

We first identified all tracking data in which birds undertook complete foraging trips. We defined a complete foraging trip as all trips that started and ended at the colony, contained at least one patch defined as foraging (below) and did not contain any gaps due to missing GPS fixes of > 30 minutes. We determined departure and return to the colony area using a 500 m buffer around the colony site, this radius accounts for non-foraging movements around the colony, such as when birds respond to disturbances, but do not depart the colony area. Additionally, this radius allows for the potential that departures occur from rafts and not from the colony itself, as any rafting observed at this colony occurs within close proximity of the colony (JPYA; personal observation). We also examined colony co-departures using 1.5, 5 and 10 minute time windows. Results for 1.5 and 5 minutes were qualitatively similar (Supplemental Figure 2.1). To allow for individuals' GPS devices taking fixes up to 60 seconds apart we selected the 3-minute time window for the presented analysis, as this attempts to minimises the selected time-window while still aiming to include co-departures that might be otherwise be missed due to device resolution. As gannets have been found

to have a very long visual range (10-40 km; Thiebault *et al.* 2014b)), even at the maximum of this time-window departing birds will still be in visual range of one another.



Supplemental Figure 2.1 Distribution obtained from 10 0000 permutations of the proportion of trips in which at least one pair of individuals co-departed within A) 1.5 minute B) 5 minute and C) 10 minute time windows compared with the observed proportion (indicated by the dashed line) of co-departures for each time-window respectively.

Behavioural classification

To identify areas in which gannets exhibit foraging behaviour during their foraging trips, we used Expectation-Maximization binary Clustering (Garriga *et al.* 2016), a method based on maximum likelihood Gaussian mixture models (Redner & Walker 1984). EMbC is an unsupervised clustering algorithm that is easily implemented and produces biologically interpretable behavioural classification from animal tracking data. It has been previously demonstrated to produce accurate results for congeneric northern gannets (Bennison *et al.* 2018). The behavioural output is derived from two input variables; turning angle and speed, calculated between successive GPS relocations. EMbC produces four behavioural classification categories, obtained from the four combinations of high and low values for the two variables. As both low speed categories were categorised by speeds below 1.5 m/s we considered these together as 'resting' behaviour, based on previous work on

gannet behavioural movements (Wakefield *et al.* 2013). We considered high speed and low turning, indicating fast straight flight, to be 'commuting behaviour', while high speed and high turning was taken to represent 'foraging behaviours' (Supplemental Table 2.1). EMbC analysis was conducted on all complete trips simultaneously using the R package EMbC v2.0.0 (Garriga *et al.* 2016), and a built in smoother function was applied to take into account temporal association in behavioural states.

Supplemental Table 2.1: Minimum and maximum speed and turning angle for each behavioural state classification using EMbC. Two states with speeds below 3 km/h where merged into a single state termed 'resting'.

Behaviour	Min speed (km/h)	Max speed (km/h)	Min turn (rad)	Max turn (rad)
Resting	0	3	0	3.14
Commuting	3	120	0	0.61
Foraging	1.7	120	0.61	3.14

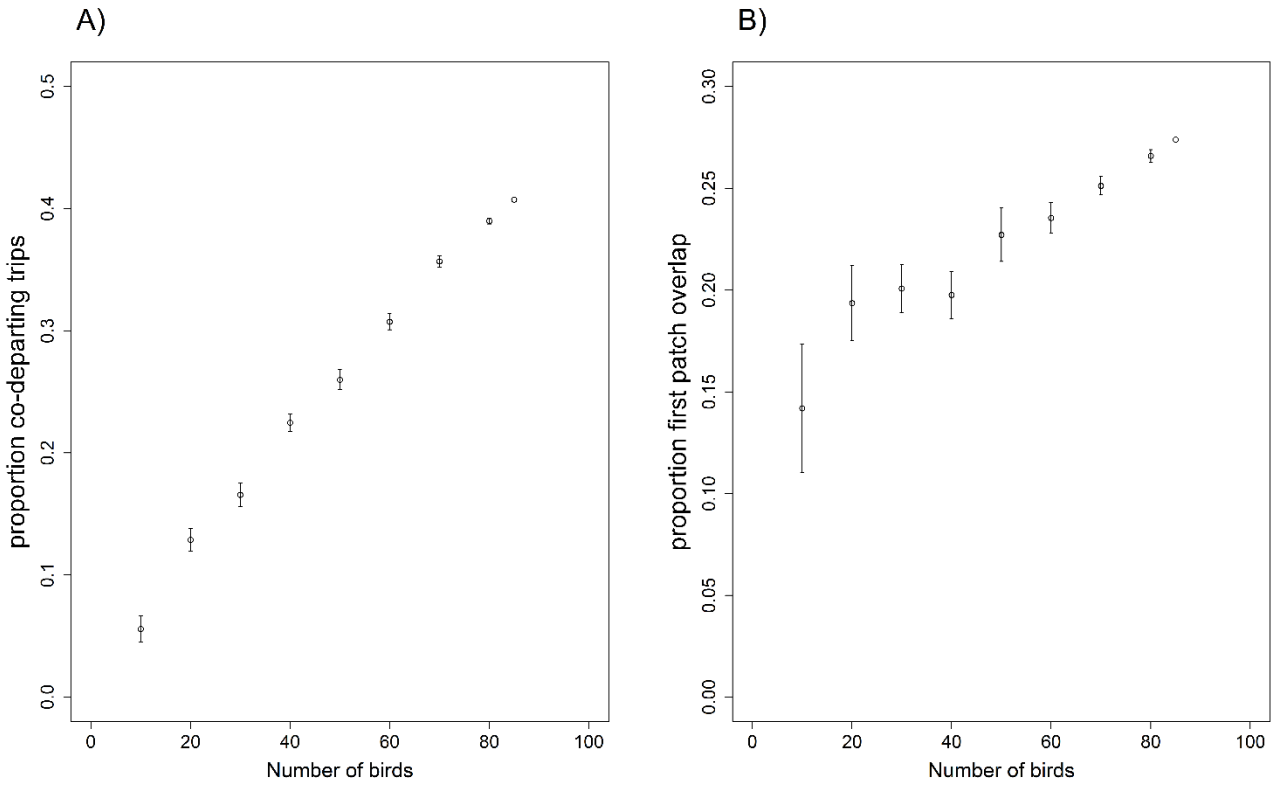
Null models

To determine if the observed patterns of co-departing behaviour could be generated simply due to random departures of individuals, we compared our observed data to null models as follows. For each colony departure we generated 10,000 permutations of each departure time, by swapping each time of departure with randomly drawn departures times from the complete dataset. This allowed each individual to maintain the same number of departures on each day across the study period, but redistributed these events to different times of the day. This method also constrained all permutated departures to observed departure times, thus controlling for the diurnal activity pattern exhibited by gannets (Garthe *et al.* 2017). For each set of permutations we then identified the trips in which the permutated departure times were found to be 'co-occurring' following the same procedure used on the observed data. We determined significance (p-values) by calculating the proportion of times the observed proportion of co-departing trips was found to be more extreme than the results obtained from the permutated datasets.

Similarly, to determine if the overlap in first foraging patches was driven purely by chance, we compared our results to null models constructed by following a similar procedure. The timing of each foraging patch was permutated 1,000 times by swapping the observed foraging time with a randomly drawn foraging patch time from within the dataset as described above. We then recalculated the temporal and spatial overlap for each permutated foraging patch following the procedure used on the observed data. Significance was again calculated as the proportion of times the observed overlap was found to be more extreme than the results obtained from the permutated datasets.

Effect of untagged individuals

To determine the impact of untagged individuals in the colony on our estimates of co-departure and first patch overlap, we resampled our data set at varying scales (10 – 80 individuals) and re-calculated overlap in colony departures and patch overlap as described previously. For each subsample, we drew the specified number of individuals from the whole data-set, and we repeated each sample 10 times (Supplemental Figure 2.2).



Supplemental Figure 2.2 Mean ± SE of proportion of A) trips that co-depart from the colony and B) co-occurring first patches that overlap in space for each subsample of the data (10, 20, 30, 40, 50, 60, 70 and 80 individuals). Final point indicates observed value for the full data set (n = 85).

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Chapter 3

Consistent sociality but flexible social associations across temporal and spatial foraging contexts in a colonial breeder

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Author contributions:

Study conceived by TBJ, SCP, JPYA and JAG. Data analysed by TBJ with coding assistance from JCE. Data collected by MARM, MRW and JPYA. Manuscript written by TBJ with support from SCP, JAG, JCE & JPYA.

Abstract

When the consequences of sociality differ depending on the state of individual animals and the experienced environment, individuals may benefit from altering their social behaviours in a context-dependent manner. Thus, to fully address hypotheses about the role of social associations it is imperative to consider the multidimensional nature of sociality by explicitly examining social associations across multiple scales and contexts. We simultaneously recorded >8000 associations from 85% of breeding individuals from a colony of Australasian gannets (*Morus serrator*) over a two week period, and examined gregariousness across four foraging states using multilayer social network analysis. We found that social associations varied in a context-dependent manner, highlighting that social associations are most prevalent during foraging (local enhancement) and in regions expected to provide clustered resources. We also provide evidence of individual consistency in gregariousness, but flexibility in social associates, demonstrating that individuals can adjust their social behaviours to match experienced conditions.

Introduction

Animal sociality presents both costs and benefits to individuals living in groups. Thus, for social behaviours to evolve it is expected that the benefits will outweigh the costs of sociality (reviewed by Krause & Ruxton, 2005; Ward & Webster, 2016). For instance, social foraging strategies are expected to evolve when group behaviour increases individual foraging efficiency and the costs of competition are low (Giraldeau & Caraco 2000; Beauchamp 2014). Similarly, during group movement, coordination will occur when benefits, such as decreased energy expenditure (Weimerskirch *et al.* 2001; Portugal *et al.* 2014) or pooled navigational ability (Berdahl *et al.* 2018), outweigh the costs incurred by consensus decision making (Conradt & Roper 2005). On an individual level, animals within a group may not experience equal outcomes from social behaviours, leading to individual differences in level of gregariousness (Krause *et al.* 2015) and therefore individuals may continuously evaluate the cost-benefit trade-off of sociality, leading to the formation and division of groups overtime (fission-fusion dynamics, Aureli *et al.* 2008). Thus, an individual's decision to participate in social behaviours may vary based on circumstances (Sueur *et al.* 2011).

Individual gregariousness may, therefore, be differently selected for between different contexts leading to social plasticity in which individuals adjust the expression of social behaviours across time or space to maximise the benefits gained and minimise the costs of social associations (Oliveira 2009, 2012; Montiglio *et al.* 2018). Social plasticity may be expected when the cost and benefits of associating differ between contexts, or when different individuals experience different social outcomes in the same context. Throughout temporal cycles, such as daily or seasonal changes, individuals experience a variety of conditions and undertake temporal changes in activity or life-history that may influence the costs and benefits received from social associations (Krause & Ruxton, 2005; Ward & Webster, 2016). However, to date, there has been little work empirically evaluating the effects of different contexts on individual variation in social behaviours. In one study of semi-feral ponies (*Equus caballus*), individuals were found to show inter-annual consistency but seasonal

flexibility in their gregariousness (Stanley *et al.* 2018), which was found to be driven by seasonal changes in male harassment related to breeding status. Similarly, the costs and benefits of sociality in any given social context may be influenced by external spatial conditions, such as resource distribution, which can also differentially impact individuals (Webber & Vander Wal 2018). For example, eastern water dragons (*Intellagama lesueurii*) vary their use of social tactics depending on their spatial location within their home range, and these differences were found to be stronger in females (Piza-Roca *et al.* 2018). Thus, individuals may vary their degree of gregariousness between social contexts depending on the context-specific trade-offs.

Alternatively, individual gregariousness may be constrained across different contexts, due to individually consistent expression of behaviours. Consistent individual differences in behaviours (termed personality) are seen across a broad range of animal taxa (Sih *et al.* 2004; Réale *et al.* 2007). Previous work has demonstrated that personality can influence an individual's social associations (Krause *et al.* 2010; Ilany & Akçay 2016), which could lead to individuals of a given personality type expressing a specific social phenotype (e.g. Croft *et al.* 2009; Aplin *et al.* 2013; Johnson *et al.* 2017). Additionally, while personality can influence an individual's gregariousness, it has also been shown in a number of studies that an individual's social position within a group may also remain consistent across time and/or contexts (Jacoby *et al.* 2014; Aplin *et al.* 2015; Firth *et al.* 2017; Formica *et al.* 2017; Krause *et al.* 2017; Kulahci *et al.* 2018), however little work has addressed such consistency in social metrics across various scales (i.e. gregariousness *vs* associations). Such consistency in social traits, such as social network position, could potentially drive consistency in other behaviours. Thus, an individual's sociality may carry-over across contexts, and may in itself reflect a social personality (Réale *et al.* 2007; Wilson *et al.* 2012).

To understand how behavioural and spatial contexts driving behavioural plasticity or consistency interact to influence individual variation in sociality it is necessary to address the multidimensional nature of animal social associations that occur across a wide-range of contexts and scales (Finn *et al.*

2019). However, despite our understanding of the complexity of factors influencing animal sociality, few studies have attempted to quantify the context-dependent influences on gregariousness and social associations, and even fewer at the fine temporal scale relevant to decision making in wild populations. Many analytical approaches to the study of animal social behaviours are generally designed to examine sociality within a single context (such as foraging or aggression) in isolation, or aggregate across contexts, losing any variation that may exists in social metrics across contexts. Recently, research has demonstrated that considering only one social context can underestimate an individuals' gregariousness. For instance, if an individual had only weak social associations in a single context, but was social across a high number of contexts, a higher measure of gregariousness would be observed when considering multiple contexts (De Domenico *et al.* 2015c; Finn *et al.* 2019). Additionally, when considering behaviours that occur with different frequencies, a single context or aggregate approach can be dominated by the most frequent behaviours (but see Silk *et al.* 2006). Only recently have studies begun to consider variation within and between social associations across multiple contexts, yet these approaches have still often analysed networks of different social contexts in separate models (e.g. Madden *et al.* 2011; Gazda *et al.* 2015; Kulahci *et al.* 2018 but see Firth & Sheldon 2016). A recently developed framework for applying multilayer social network analysis to ecological research (Silk *et al.* 2018; Finn *et al.* 2019) allows researchers to implicitly consider the multifaceted nature of social associations to more fully understand the complex role of sociality in group living animals.

Coloniality is an extreme case of group living where large aggregations of individuals at breeding or roosting sites provide significant opportunities for social associations across a range of behaviours. Indeed, the high availability of social information in these aggregations has been highlighted as an important mechanism in the formation and maintenance of colonial living (Danchin & Wagner 1997; Evans *et al.* 2016). Thus, colonial species, such as 95% of seabird species (Coulson 2001), present interesting systems in which to examine individual sociality across multiple contexts. During the breeding season, seabirds make numerous trips between the colony and variable foraging areas.

Previous studies have shown seabirds can form groups at the colony during outward travel (Daniel *et al.* 2007; Weimerskirch *et al.* 2010; Machovsky-Capuska *et al.* 2013; Jones *et al.* 2018) and during commuting travel between colony and foraging locations (Berlincourt & Arnould 2014; Thiebault *et al.* 2014a; Tremblay *et al.* 2014), which can allow the colony to act as a centre for foraging information, and can lead to individuals engaging in following behaviour (Harel *et al.* 2017). At sea, seabirds are also known to form foraging aggregations (Coulson 2001; Evans *et al.* 2015; Cook *et al.* 2017), and evidence from experimental and modelling approaches have demonstrated these aggregations can provide social information by attracting individuals to a foraging locations through the observation of other foraging individuals (local enhancement) (Buckley 1997; Thiebault *et al.* 2014b; Bairos-Novak *et al.* 2015; Boyd *et al.* 2016). However, it remains unclear to what extent these aggregations indicate active social choices in comparison to patterns emerging due to shared space use associated with a clumped resource. Furthermore, due to the vast number of individuals in many colonies and large spatial scales covered by seabirds, there has been limited direct quantification of the importance of individual variation in the use of social strategies.

In this study, we provide a unique direct quantification of the variation in individual gregariousness and assess consistency of social associations across multiple foraging contexts and scales (overall gregariousness *vs* dyadic associations) using a novel multidimensional network approach. We collected data simultaneously from 85% of the actively breeding individuals from a small colony of Australasian gannets (*Morus serrator*; hereafter gannets) and examined four key foraging states: (1) colony co-departures, (2) commuting movements, (3) foraging movements and (4) colony co-returns. Gannets, like many colonial seabirds, frequently associate with both conspecifics and heterospecifics at sea (Vaughn *et al.* 2010), and have been shown to associate during colony departure (Jones *et al.* 2018) and while rafting (Carter *et al.* 2016). Specifically, we aim to quantify the prevalence of aggregations in gannets across four foraging states. We employ null models that account for individual spatial patterns to determine the extent to which these aggregations represent social associations and quantify the inter-individual variation in gregariousness. By

examining the patterns of association across the entire foraging trip, we are able to test the hypotheses that the colony or foraging sites (or both) are important locations of social foraging associations. We predict that if individuals form social associations during colony departure this provides evidence in support of the idea that social foraging information can be transferred at the colony site. If local enhancement is a key social foraging behaviour, we predict a high level of associations during foraging.

To test the hypothesis that individual sociality is influenced by behavioural contexts and scale we assess the pattern of associations across four foraging states at two levels; overall social tendency (gregariousness) and the persistence of dyadic associations. On an individual level, we assess individual consistency in gregariousness and measure the overlap in specific social associations between each foraging stage. If individuals maintain a high overlap between social associations during colony departures, commuting and foraging states indicating overall consistency in their choice of associates across the foraging stages, this would provide evidence that information may transfer across foraging state (i.e. colony as a location of information transfer), as social associations will need to be maintained across the foraging trip. We further predict that low overlap between foraging and other states would provide evidence that foraging associations form at prey patches, indicating that local enhancement is a prominent social tactic.

Finally, gannets from this colony are known to undertake location-specific foraging strategies, in which some individuals specialise on foraging within a shallow inshore bay area with larger solitary prey, and others forage predominantly in the deeper off shore strait in which they encounter small shoaling prey (Wells *et al.* 2016). This allows us the opportunity to simultaneously test the hypothesis that gregariousness will vary with these different location-specific foraging strategies. We predict that when social associations are related to foraging benefits, gregariousness will vary depending on resource type and distribution, with individuals displaying higher levels of gregariousness when prey is clustered and less predictable.

Methods

Study system and behavioural classification

The study was conducted at the Pope's Eye colony located in Port Phillip Bay, south-eastern Australia (38°16'42"S, 144°41'48"E), in January 2015, during the chick rearing period. We recorded location data (2 minute resolution) from 85 birds, accounting for 85% of the active breeders in the colony at the time. Analyses were restricted to complete foraging trips during the period of maximum overlap in individuals with concurrent GPS tracking (January 9-22 2015). During foraging trips, seabirds undertake several distinctive behaviours which can be inferred from location data using hidden Markov models (HMM, as in Dean *et al.* 2013; Grecian *et al.* 2018). We identified three behaviours, which represent 1) fast directed commuting flights, 2) slower tortuous foraging movements and 3) resting at sea. For additional details of GPS deployment and behavioural classification see the Supplemental Materials.

Social associations

To identify social associations from the GPS data we extracted the temporal and spatial co-occurrences of individuals separately for departing, commuting, foraging and returning (Supplemental Figure 3.1). Individuals were defined as associating during colony departure or return, when either co-departing or co-returning to the colony within three minutes of another individual and with a difference in angle of travel less than 45° (see supplemental materials for further details on threshold selections). We next defined commuting associations by applying a distance, time and heading threshold to periods defined as commuting from the HMM approach. Gannets were considered to be associating during commuting if they were travelling within 1500 m of one another for > 5 minutes, a distance that is well within the visual range of gannets (Thiebault *et al.* 2014b). Here again, we considered only associations in which the difference in angle of travel was less than 45°. We defined a foraging association using a distance and time threshold only, as angle of travel varies greatly during foraging. Individuals were considered to be associating if they were recorded

within 500 m for > 5 minutes during fixes that were classified as either foraging or rest, as individuals resting on the water may still provide foraging cues, especially as resting often follows or precedes a bout of foraging (Ropert-Coudert *et al.* 2004). Only associations in which one or both individuals were classified as foraging were retained in the social network analysis to ensure rest-rest associations were not included in the foraging network.

For each foraging individual we determined the proportion of an individual's colony departures, returns, commuting and foraging bouts that were classified as associating. To quantify individual sociality during each foraging state we used social network-based techniques (Krause *et al.* 2015). For colony co-departure and co-return networks we defined an edge (connection between a pair of individuals) by the number of co-departures and co-returns made by each dyad respectively. For the co-commuting and co-foraging networks associations generally did not last the length of an entire commute or foraging bout, thus we defined edges by the sum of the duration of associations for each dyad. As we have complete tracking data on all individuals studied, raw association values were used to construct networks (Hoppitt & Farine 2018). To ensure common scale across the networks and to control for differences in frequencies of behaviours, all edge weights were scaled between 0-1 (0 being the lowest value, and 1 the maximum value or duration of associations respectively).

For each network we calculated the network density (ratio of observed edges to all possible edges) and calculated the degree and weighted degree centrality (hereafter weighted degree) for each individual; network measures were calculated using igraph v. 1.2.4.1 (Csardi & Nepusz 2006). Degree is the total number of associates an individual has and weighted degree (also known as strength) is a measure of the number and strength of an individual's associations and can be seen as a general metric of the gregariousness of an individual (Wey *et al.* 2008). Given the low number of repeated associations over our study period between the same individuals during co-departures, returns and commuting, we did not assess preferential associations between individuals within each foraging state and instead assessed an individual's general level of gregariousness.

To examine how the networks for each state relate to one another, we used a multi-layer social network (Silk *et al.* 2018; Finn *et al.* 2019), in which each set of associations represents a separate layer within an overall network structure. In particular, we used a multi-relational multiplex network in which each layer represents the same (or a subset of the same) individuals in a different social context, in this case the four foraging states studied, (Finn *et al.* 2019) and the connections between layers connect individuals to themselves in other layers. Additionally, to assess how social associations are linked across contexts, we constructed an additional final network layer (hereafter called the 'outcome' layer) in which we defined social associations based on a shared outcome of a previous social association (i.e. joint commuting leading to foraging, or joint foraging leading to commuting). For this network layer, an association was defined as any association that either 1) started at a shared origin (either a foraging patch or the colony) and resulted in joint commuting or 2) started in a joint commute and ended at a shared destination. Edge weights were again defined as the number of associations of each dyad scaled between 0-1 as above.

Location-specific foraging strategy

Gannets breeding at Pope's Eye colony exhibit distinctive location-specific foraging trips characterised by different environmental features (Wells *et al.* 2016) and previous work in this population has shown that individuals are consistent in their location-based foraging (Angel 2015). We identified three different trip types from the data; 1) trips with >70% of fixes within Port Phillip Bay (bay trips), 2) trips with >70% of fixes outside of the bay (strait trips) and 3) trips with <70% of fixes in either the bay or strait (switch trips) (Figure 3.1). Individuals were then classified as bay or strait specialists if >70% of trips were defined as bay or strait trips respectively, with all other individuals classed as 'switch' individuals (as in Rodríguez-Malagón 2018) (Supplemental Table 3.1).

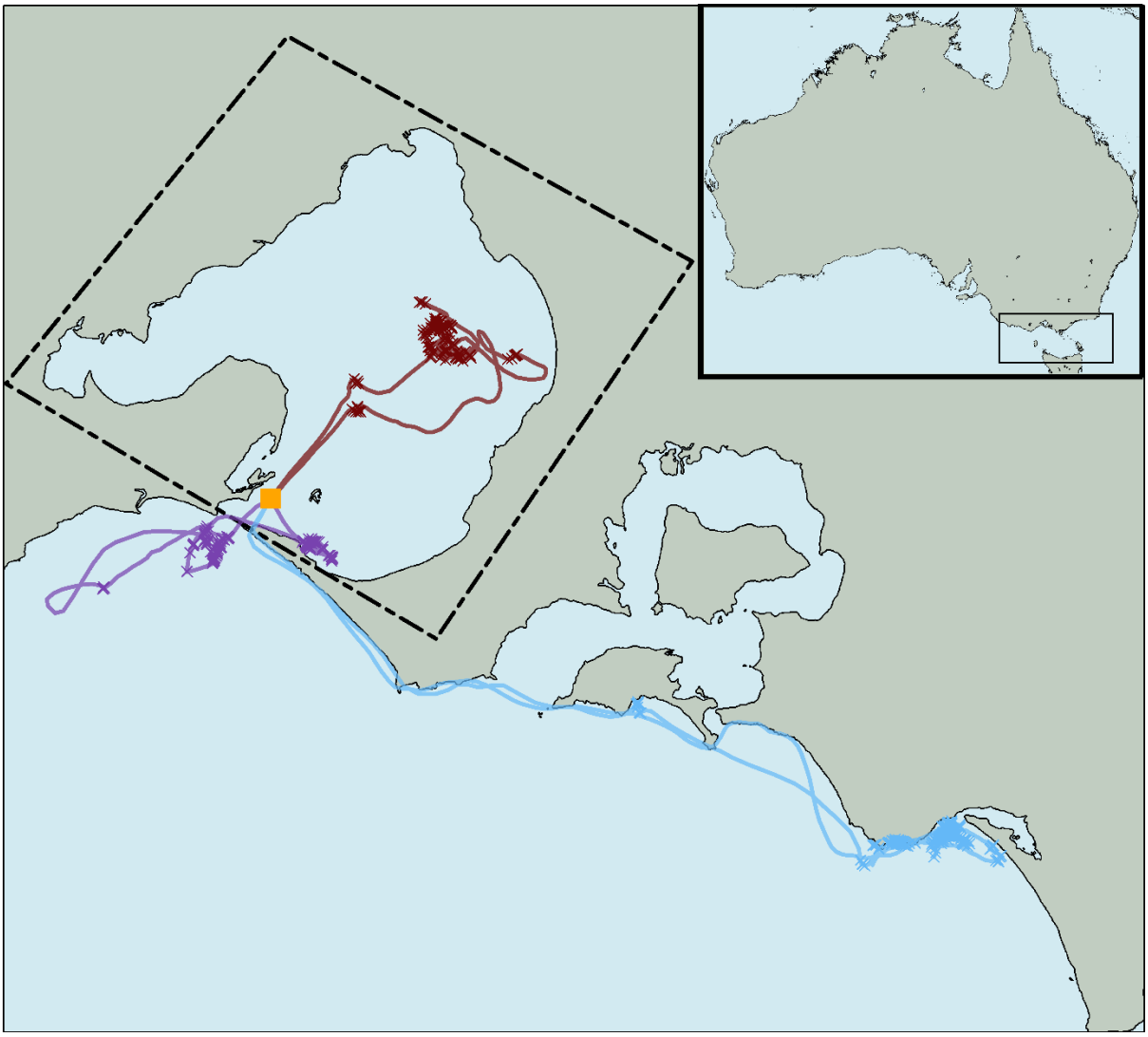


Figure 3.1: Map of the study area around Pope's Eye gannet colony, located in Port Phillip Bay, Australia. The colony site is represented by the orange square. Example foraging trips are shown for a bay specialist (red), a strait specialist (blue) and a switch individual (purple) with the area used to define the bay shown by the dashed box. Foraging locations as identified via hidden Markov models are marked on each trip by crosses. Insert shows Australia, with the colony and surrounding foraging area marked with a box.

Statistical analysis

Null models

To examine if social associations during each foraging state were observed more often than expected by chance, we compared the network density and the observed weighted degree to null models obtained from data-stream permutations of the GPS data for each of the four networks

(Farine 2017). Unlike typical data-stream permutations, to maintain an individual's specific movement patterns, we randomised GPS data within individuals by randomly swapping the day each trip occurred on. This method conserved individual differences in spatial movement, while breaking the temporal association of the data (Spiegel *et al.* 2016), allowing us to determine if co-occurrences are driven by active group formation or a by-product of persistent use of the same space. After each permutation we recalculated the departure, commuting, foraging and returning associations as described above. We then compared the observed network density and mean weighted degree from each network to the distribution of network densities and weighted degrees obtained from 1000 permutations of the data, respectively. P-values were obtained as the proportion of times the values obtained from the permutated data were more extreme (larger) than the observed value.

Individual gregariousness across foraging contexts

To determine if individuals expressed flexible or consistent gregariousness across foraging states we used the network based consistency analysis as described in Wilson et al. (2012). This network-specific method is used to account for the non-independent nature of association data. As this method is designed to assess the change in relative position of individuals rather than the absolute value of weighted degree we first determined the ranked weighted degree within each observed network. We then computed the sum of each individual's variance in ranked weighted degree across the observed departure, return, commuting and foraging networks (SV_O). We then compare the observed value SV_O to the sum of variance values obtained from calculating the variance in ranked weighted degree from the null models obtained from 1000 permutations (SV_R). As a low value of SV_O demonstrates that the relative ranking of individuals across networks is consistent, significance was calculated as the proportion of SV_R values from the data permutations that were more extreme (lower) than the observed SV_O.

Variation in social associations across foraging contexts

Next, to assess how individual social associations vary across foraging states and to determine how these different portions of the foraging trip are linked through the outcome network, we assessed the similarity in network structure between the four network layers. We computed the edge overlap between layers in the multiplex social network using the software MuxViz (De Domenico *et al.* 2015b), which quantifies the proportion of common links between dyads that are conserved between network layers, as a measure of how social associations are carried over between contexts. This method considers weighted network edges and gives a measure of consistency in dyadic associations across contexts. We also calculated the pair-wise correlation between network layers by using Mantel tests to calculate the similarity between the respective association matrices (Smouse *et al.* 1986), as this method has frequently been used to assess the correlation between matrices. However, this method may be strongly impacted by zero values as matrices must be the same size for comparison (thus non-interacting individuals in one layer must be included in all layers for comparison).

Variation in gregariousness across spatial contexts

To assess how between individual gregariousness varied across location-specific foraging strategies, we repeated the analysis comparing mean weighted degree to the corresponding null models for each of the three spatial foraging strategies separately (bay, strait and switch). As the bay specialists were a small male-only subgroup of the study population, we repeated the network consistency analysis and edge overlap analysis for a multi-layer network constructed as described above, but excluded the bay-specialist individuals. All statistical analyses were performed in R v.3.5.1 (R Core Team 2016). Additionally, to determine how spatial context is reflected in the social organisation of individuals, we conducted a network clustering analysis for community detection (as in Finn *et al.* 2019) using MuxViz (De Domenico *et al.* 2015a; multilayer InfoMap method, see Supplementary

Materials for additional details). In this approach, we assess if social clusters detected correspond with the location-specific foraging strategies.

Results

Social associations

In total, we recorded 2877 hours of commuting, 4398 hours of foraging and 6717 hours of resting behaviours. From this data, we detected 173 colony co-departures, 199 colony co-returns, 477 commuting associations and 7738 foraging associations. Associations during commuting were the least frequently observed behaviour, with foraging, colony co-departures, and co-returns occurring at higher rates (mean proportion of social bouts per individual; commuting = 0.13, foraging = 0.32, co-departures = 0.28, and co-returns = 0.31). The patterns of associations were found to vary between foraging states (Figure 3.2).

For all four states studied, the observed network density was significantly greater than the density obtained from the null models indicating all networks were more connected than expected compared to the null (Table 3.1). The density of the foraging and commuting networks had the greatest differences to the corresponding null models (Supplemental Figure 3.5). Similarly, both mean degree (number of associates) and mean weighted degree (strength of associations) were found to be significantly larger than expected given the null models, and there was high between individual variation in the number and strength of associations expressed as degree and weighted degree (Table 3.1, Supplemental Figures 3.6&3.7). Again, the number of associates during foraging was found to have the greatest difference from the null model.

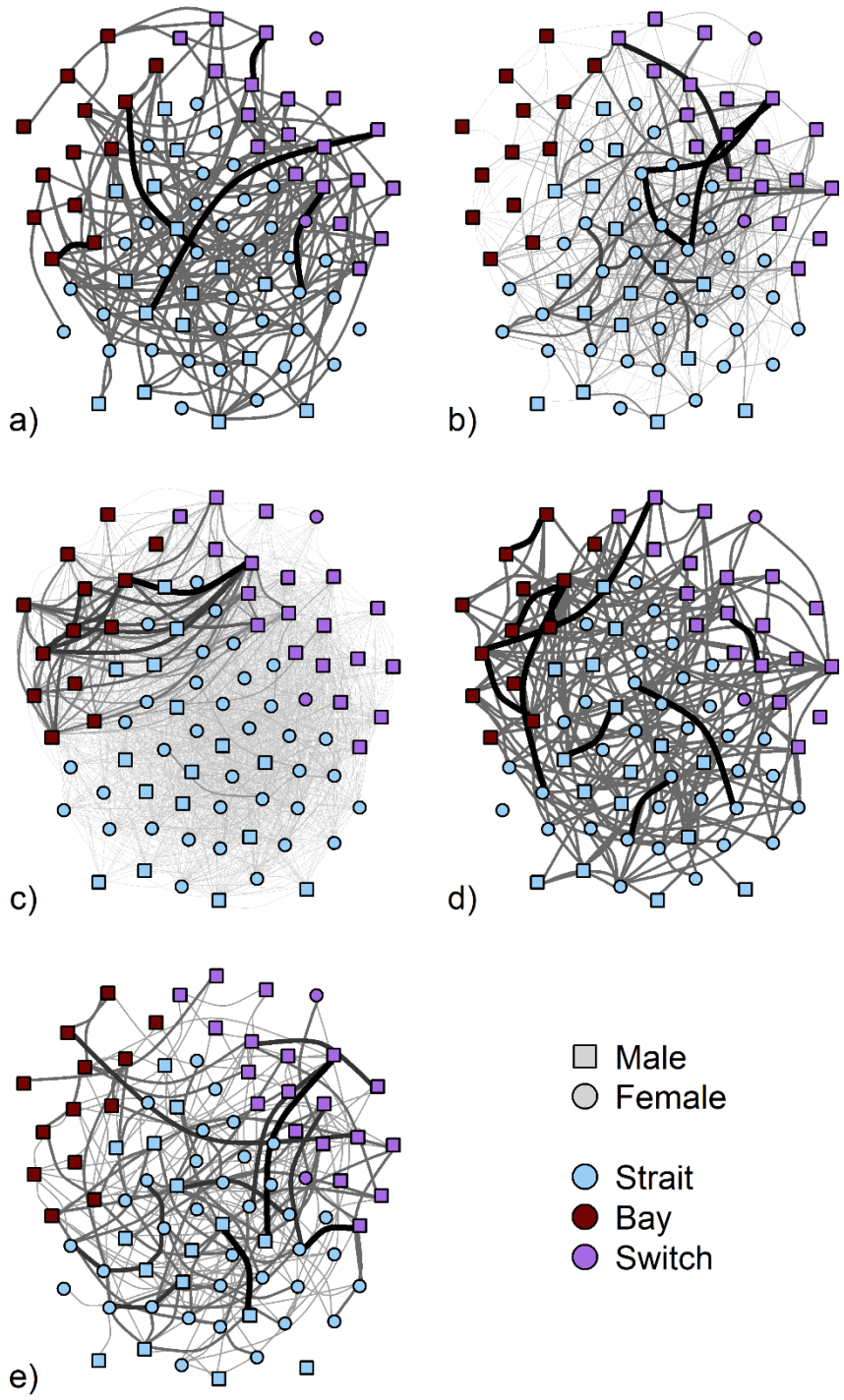


Figure 3.2: Gannet social networks from associations during a) colony co-departures, b) commuting, c) foraging, d) colony co-return and e) 'outcome' network layer in which associations represent the carry-over outcomes of associations (i.e. joint commutes that end in foraging/colony or foraging/colony co-occurrences that end in commuting). Males are represented by squares and females by circles. Bay specialist are shown in red, strait specialist in blue and individuals that did not specialise ('switch' individuals) shown in purple. Edge weights are scaled in thickness from the minimum (lightest line) to maximum (darkest line) association strength recorded in each given layer.

Table 3.1: Summary of network metrics for each foraging stage network. Network density, mean degree and mean weighted degree are given. For mean degree, the number of associates, and mean weighted degree, a general metric of gregariousness, the range of individual values observed are given in parenthesis. All metrics are compared to the distribution of values obtained from 1000 network permutations and p-values are given as the proportion of times the permutated values were more extreme (higher) than the observed value.

Foraging State	Network density	p-value	Mean degree (range)	p-value	Mean weighted degree (range)	p-value
Co-departure	0.05	**0.02**	3.95 (0-13)	**<0.001**	2.04 (0-7.0)	**<0.001**
Commuting	0.11	**<0.001**	9.67 (0-23)	**<0.001**	1.64 (0-5.2)	**<0.001**
Foraging	0.46	**<0.001**	39.1 (3-64)	**<0.001**	1.89 (0.1-9.1)	**<0.001**
Co-return	0.05	**0.004**	4.45 (0-18)	**<0.001**	2.34 (0-10.5)	**<0.001**

Individual gregariousness across foraging contexts

The observed sum of variance calculated from weighted degree, was significantly lower than the sum of variances obtained from the null model permutations (SV_O = 5.64, SV_R range = 5.19-7.99, p = 0.012), indicating that individuals were consistent in their relative sociality across foraging contexts.

Variation in social associations across foraging contexts

Of the observed social associations, we recorded 287 'outcome' events resulting from a social association carrying-over from one foraging state to another, providing evidence of direct temporal carry-over of social associations from one foraging state to a subsequent state. Joint foraging, from associations formed at the foraging patch, that led to co-commuting was the most frequent observed outcome (32% of outcomes) followed by co-commutes, where individuals formed an association in flight, that then resulting in co-foraging (29% of outcomes). Both colony co-departures leading to commuting, and co-commuting ending in the colony accounted for 19.5% of outcomes each. In all cases, an instance in which carried over across three states (i.e. forage to commute to forage) was considered as two separate incidents (i.e. one forage leading to commute and one commute leading to a forage) for analysis purpose.

There was generally low edge overlap between all behaviour layers, with the highest edge overlap being between the foraging and commuting layers and between the foraging and return layers (Figure 3.3). This indicates low consistency in dyadic associations between behavioural states and that birds associating with individuals in one context do not associate with the same individuals in another. When comparing the results from the multilayer edge overlap to pair-wise correlations between the association matrices using Mantel tests, we found generally similar results (Supplemental Table 3.2). However, the Mantel test identified very low correlation between the commuting and foraging matrices, despite the relatively higher edge overlap found between these two layers. This may result from including individuals that only had associations in one layer, but were absent from another layer, as this would drive down the correlations. By contrast in the edge-overlap approach, these occurrences would be considered as edges that were not preserved between the two layers.

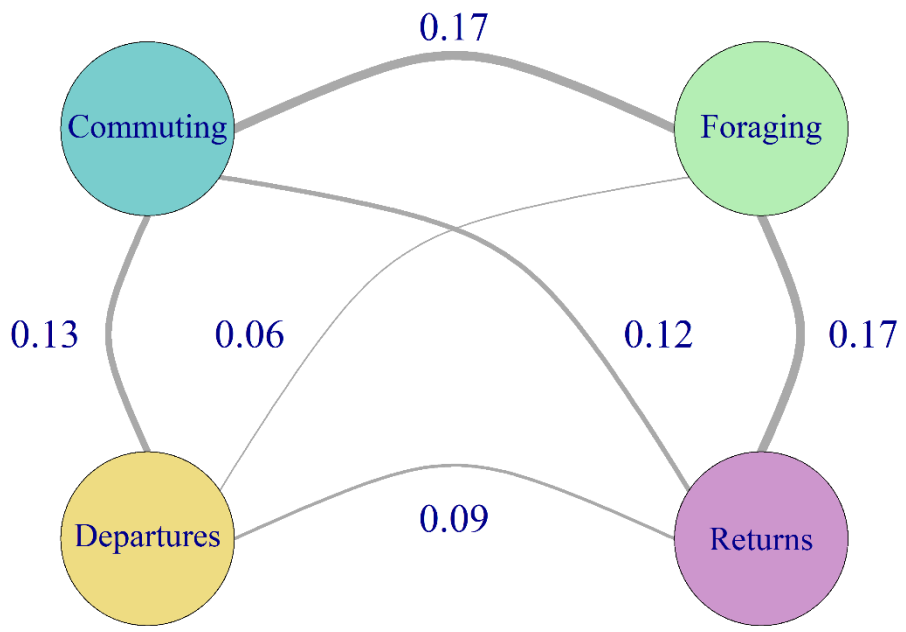


Figure 3.3: Multilayer edge comparison of foraging state layers depicted as a network with nodes representing each state (departure, commuting, foraging and returns) from the multilayer gannet social network. Edge values represent the proportion of shared edges between pairs of layers, which is a measure of the consistency of dyadic social associations across contexts.

Variation in gregariousness across spatial contexts

When considering the spatial foraging strategies separately, gannets that restricted their trips to the bay were found to not have a higher weighted degree during colony co-departures and foraging than expected by chance (Table 3.2, Figure 3.4). This analysis indicates that the spatiotemporal overlap of bay individuals during colony co-departures and foraging is not greater than is expected in comparison to the spatial null models, meaning bay gannets did not form social groups at a rate higher than expected given their spatial use of the bay. In contrast, for all other foraging states and spatial strategies, we found the overall pattern remained, with the mean weighed degree significantly higher than expected given our null models. As individuals within the bay were found not to associate at a higher rate than expected from our null models, we repeated the analysis of individual consistency and overlap in social associations across foraging states excluding bay-only individuals and obtained similar results to our whole network analysis (Consistency in sociality for non-bay individuals: $SV_O = 4.56$, SV_R range = 4.19-6.93, $p = 0.002$, edge-overlap analysis: Supplemental table 3.3).

Using InfoMap community detection approaches we found that when considering each layer separately, the foraging network best predicts the location-based strategies of individuals. The foraging network consisted of two communities; one community composed exclusively of bay and switch individuals and the second community composed of strait and switch individuals and two bay foragers (Supplemental Figure 3.9). Using multilayer community analysis, we found similar results to the foraging layer alone, with all four layers showing the same general pattern of bay specialist and strait specialist clustered in different communities (Supplemental Figure 3.9).

Table 3.2: Mean weighted network degree, a general metric of gregariousness, during colony departures, returns, commuting and foraging behaviours, across the three spatial foraging strategies (bay; >70% of trips within Port Phillip Bay, strait; >70% of trips outside the bay, and switch; <70% of trips in either category), compared with weighted degrees obtained from 1000 network permutations.

Behaviour	Observed mean weighted degree	Range of mean weighted degree from permutations	p-value
Departure			
all	2.04	0.94-1.66	**<0.001**
bay	1.92	0.88-2.50	0.11
switch	2.23	0.84-2.13	**<0.001**
strait	1.98	0.81-1.62	**<0.001**
Commuting			
all	1.64	0.28-1.39	**<0.001**
bay	0.73	0.10-1.20	**0.028**
switch	1.62	0.22-1.39	**<0.001**
strait	1.88	0.29-1.47	**<0.001**
Foraging			
all	1.89	0.88-1.49	**0.001**
bay	4.15	3.50-6.12	0.86
switch	2.11	1.04-1.89	**0.001**
strait	1.23	0.11-0.24	**0.001**
Return			
all	2.34	1.08-1.72	**<0.001**
bay	4.08	1.25-3.63	**<0.001**
switch	2.19	0.83-2.00	**<0.001**
strait	1.96	0.79-1.74	**<0.001**

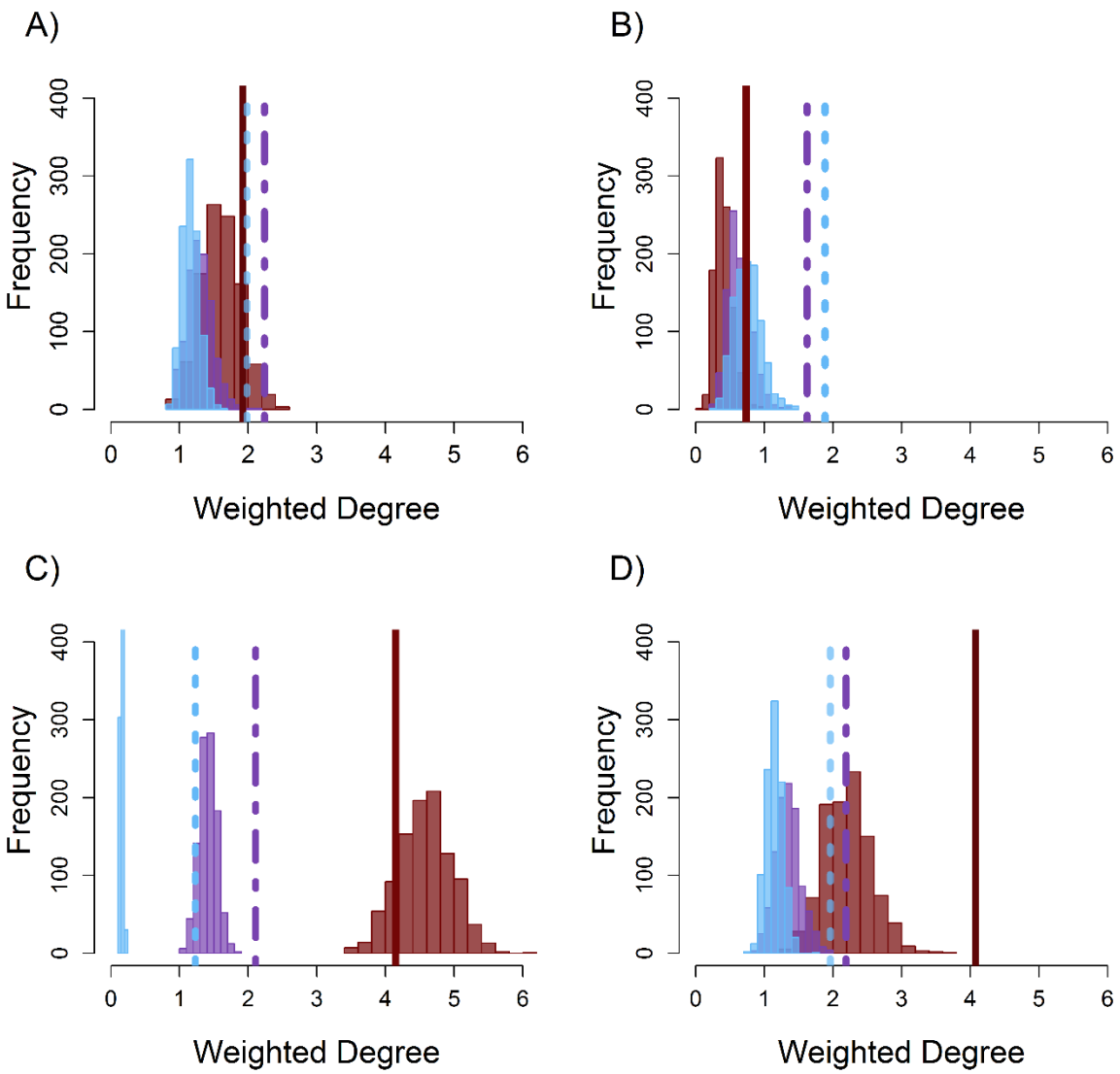


Figure 3.4: Distribution of mean weighted network degree, a general metric of gregariousness, from 1000 data-steam permutations for A) colony co-departures network layer, B) commuting network layer, C) foraging network layer and D) colony co-returns network layer. Lines indicate observed mean weighted degree, with strait specialist shown in blue (dotted), bay specialist in red (solid) and switch individuals in purple (dash).

Discussion

We provide a novel quantification of sociality across multiple contexts and scales demonstrating that individuals express consistent gregariousness across behavioural contexts and flexibility in social associations using a recently developed multilayer network analysis. Our results highlight that sociality needs to be measured across contexts and scales (associations *vs* overall social tendency) to fully understand how individuals adjust their use of social behaviours. Specifically, we demonstrate that the spatiotemporal overlap between individuals occurs more often than expected by chance,

while controlling for the specific spatial movement patterns of individuals. We thus, provide strong evidence that individuals actively associate socially during colony departure, foraging, commuting and colony return, although these relationships are formed opportunistically with available birds allowing individuals to maintain consistent levels of gregariousness in a highly variable social environment. Additionally, when we consider how gregarious tendencies vary across spatial contexts, we find that social decisions during colony departure and foraging are mediated by spatial foraging strategy, with bay-foraging individuals having a non-significant level of gregariousness in comparison to the null models, indicating that individuals match their tendency to be social to the conditions they experience. This is further evident in the community structure underlying the foraging and multi-layer networks, in which the community clusters detected strongly match the individual spatial foraging strategies.

We found strong evidence that gannets engage in social behaviours across four foraging contexts studied (colony departure, commuting, foraging and colony return) and that individuals are consistent in their relative weighted degree, a measure of gregariousness or tendency to be social. This finding demonstrates that individuals are consistent in the expression of social behaviours across multiple foraging contexts. Our study adds to the findings of several recent studies highlighting that individuals may express consistency in sociality across contexts (Firth & Sheldon 2016; Formica *et al.* 2017; Krause *et al.* 2017; Kulahci *et al.* 2018), providing further evidence that individuals may express consistent levels of gregariousness that may itself be considered a social personality.

Although we demonstrate that individuals express overall consistency in their level of gregariousness across foraging contexts, our analysis at the level of social associations demonstrates that relationships between gannets were generally not preserved between different foraging contexts. Our finding of low edge overlap (multi-layer analysis) and low correlation (Mantel test) between behavioural contexts indicates that gannets form flexible social associations that vary between

foraging contexts. Previous studies in seabirds have often inferred that joint departure from the colony represents social information transmission between individuals (e.g. Weimerskirch *et al.* 2010; Racine *et al.* 2012) and recent works have demonstrated that individuals co-departing together can share foraging areas (Cook *et al.* 2017; Sutton *et al.* 2017; Jones *et al.* 2018). Our study demonstrates that although social associations formed across four foraging contexts, there was only small carry-over in specific associations across contexts. However, our network of social outcomes does show that in some cases associations formed in one context do directly carry over to a subsequent context. This result, paired with the relatively higher edge overlap found between the commuting and foraging layers provides some support for the idea that individuals could benefit from either combined search effort (Beauchamp 2014) or potentially follow conspecifics to food patches (as in Harel *et al.* 2017). However, the use of these behaviours may be highly opportunistic, due to constraints such as individuals waiting for their mate to return prior to being able to depart, which undoubtedly limits the overall frequency observed. Additionally, the fact that relatively few social connections were maintained between states suggests that social associations frequently form independently during each foraging state. Thus, our finding suggests that there may be additional benefits to the coordination of movement beyond immediate foraging gain, such as decreased movement costs from group flight (Weimerskirch *et al.* 2001; Portugal *et al.* 2014), although given the spatial and temporal resolution of our data we were unable to test for such benefits. Given the observation that joint commuting behaviour ending in a co-return to the colony occurred as frequently as co-departure leading to commuting, this could provide some evidence to further support the idea that coordinated movement provides flight benefits, as there is no foraging benefit to coordinating colony returns. Furthermore, our results suggest that perhaps consistency of social associations are not required for information transmission in this case, as individuals may respond to information from any conspecific source rather than attending to specific individuals, particularly as the scale of these associations occurs over a distance range that may not allow for individual recognition. Therefore, our results show that while social behaviour at the colony and during

commuting may contribute to social foraging information, these behaviours also present alternate social benefits.

Local enhancement, where individuals are attracted to actively foraging conspecifics (Pöysä 1992), has been modelled as an important social foraging tactic in colonial seabirds (Boyd *et al.* 2016). Here we demonstrate strong evidence for the importance of the use of local enhancement as we find a high frequency of social associations during foraging behaviour, beyond what can be explained by shared space use at foraging patches. In the case of small colonies, modelling work demonstrates that social behaviours will be limited by available opportunities (Grünbaum & Veit 2003; Boyd *et al.* 2016). For instance, while we tracked 85 birds only half this number will be on a foraging trip at any one time, as one partner generally attends the chick at all times during this period. In particular, behaviour at the colony and commuting may be especially limited, for instance as individuals are constrained in their ability to depart the colony by their partner's return and commuting opportunities are transient. Thus, for smaller colonies, local enhancement may be the favoured form of social information acquisition, over information acquisition at the colony, especially in species such as gannets that have highly visible white plumage (Bretagnolle 1993) and forage using plunge dives (Weimerskirch *et al.* 2010) that can be detected at a large distance given the high visual range of gannets (Thiebault *et al.* 2014b). Furthermore, heterospecific group foraging may also be of relatively higher importance to small colonies, which have limited conspecific social opportunities, which is something that remains to be examined.

When examining how sociality varies with external conditions, we found that for bay specialists there was no evidence of individual gregariousness beyond the level expected by chance, during colony departures and foraging, when controlling for individual spatial patterns within the bay. In fact, when compared with the null models, the observed overlap between bay-foraging individuals trended toward occurring less than expected by chance. This novel finding, adds to only one other study that addresses how social behaviours may vary in response to spatial features of the habitat

(Piza-Roca *et al.* 2018), and builds on the idea that integrating our understanding of individual social behaviours and spatial ecology is necessary for understanding a broad range of ecological and evolutionary processes (Webber & Vander Wal 2018). Although these individuals foraging within the bay represent a small proportion of the population, it is interesting to note that gannets from this colony have been shown to target different prey when foraging in these different areas, with large non-schooling fish dominating the prey obtained within the bay and small schooling fish providing the main prey items outside the bay (Wells *et al.* 2016). Such spatially driven differences in prey have also been observed in related northern gannets, with inshore large non-schooling prey being found to provide a more spatially predictable resource (Garthe *et al.* 2007). Our finding of a lack of social associations in bay foragers indicates that there are either high costs and/or low benefits to foraging socially in the bay. This matches with the predictions of social foraging theory that social foraging is most beneficial when foraging resources are less predictable and competition is low, as is the case of schooling fish (Barta & Szép 1992; Giraldeau & Caraco 2000; Beauchamp 2014). Indeed, gannets foraging on aggregated prey have been shown to have higher prey capture rates when attacking within seconds of a previous dive, indicating that when targeting schooling prey, foraging success may be actively enhanced by social foraging (Thiebault *et al.* 2016), while no such benefit will be expected for solitary prey. Furthermore, it has been recently shown that although capture success is lower in solitary foraging gannets, profitability of prey items was higher, highlighting that there are trade-offs between social and solitary foraging (Cansse *et al.* 2020). Thus, our findings highlight the context-dependent use of social strategies depending on the conditions experienced.

In summary, we simultaneously recorded the foraging behaviour of a large majority of a colonial breeding population across multiple foraging contexts, allowing us to examine how context and individual behavioural variation influence individual social behaviours. We then employed a novel multilayer social network approach to assess how social associations vary across contexts. Our findings provide strong evidence that individuals are consistent in their level of gregariousness but

show flexibility in their choice of associates. We also provide evidence of the context-dependent use of social strategies both across social contexts and with different habitat use. These findings suggest that individuals are able to adjust their social associations in response to the available opportunities, while expressing consistency in gregariousness. Lastly, we highlight the importance of the use of local enhancement at foraging patches and opportunistic social associations across co-movement behaviours. Future work that is able to directly quantify the energetic or fitness trade-offs during both search and capture portions of foraging provided by social associations under different contexts is necessary to further understand the drivers of sociality in animal groups.

Supplementary Materials

GPS logger deployment

Over a 3 day period, breeding adult gannets (n=100) were captured at the nest by hand and weighed using a suspension scale (± 25 g, Salter). To collect data on foraging trips we fitted each gannet with a GPS data logger (igotU GT-600. Mobile Action, Taiwan, 26.6 g, <1.7% of total body mass) which recorded a location fix every 2 min. Loggers were sealed in heat shrink tubing and attached to central tail feathers by water-proof tape (Tesa 4651, Beiersdorf AG, Germany). This placement was used to minimise logger impacts to hydrodynamics during plunge diving (Ropert-Coudert *et al.* 2009). We then released birds back on the nest with total handing time lasting less than 6 minutes. Birds were recaptured, approximately 2-3 weeks after deployment to retrieve loggers, and were weighed and morphometric measurements taken with handling time lasting less than 15 min. All animal handling followed protocols approved by Deakin University AEC (Approval B20-2013) and Department of Environment and Primary Industry (Victoria, Australia) Wildlife Research Permit 10006878.

Behavioural classification

We defined foraging trips as any excursion beyond a 500 m buffer around the colony that was > 30 mins in duration, to exclude brief departures from the colony due to disturbance (as in Jones *et al.* 2018). We also filtered the data to remove any trips that contained large periods of time in which no GPS fix was received (gaps > 30 min; 7 trips excluded by 7 different individuals), in total these excluded points accounted for 7.5% of the recorded GPS fixes, and accounted for less than 1% of trips. We analysed 985 trips, with individuals making between 1-28 trips each (median = 11 trips). To ensure regular sampling intervals (for classification of at-sea behaviour) and simultaneous point sampling (for social analysis), the GPS tracking data was first linearly interpolated to 1 s intervals using the package adehabitatLT v. 0.3.23 (Calenge 2006) and then resampled back to simultaneous 2-min time intervals.

We used a hidden Markov model to infer foraging behaviour from movement (Patterson *et al.* 2008) based on the distribution of step lengths and turning angles between subsequent GPS fixes. This approach has been used successfully in several species of seabirds including gannets (For example; Dean *et al.* 2013; Bennison *et al.* 2018; Grecian *et al.* 2018; Trevail *et al.* 2018; Austin *et al.* 2019). We used a gamma distribution for step length and a von Mises distribution for turning angle. We then used the Viterbi algorithm to initially estimate the most likely behavioural sequence from the GPS data. Our model revealed a three behavioural state HMM, which coincides with previous findings for northern gannets (*Morus bassanus*; Bennison *et al.* 2018; Grecian *et al.* 2018). The three defined behaviours are characterised by 1) long step lengths with low turning angles (fast directed commuting flights), 2) moderate step lengths with high turning (foraging) and 3) low step length with low turning angles (resting at sea). Additionally, to avoid breaking up continuous behaviour segments when the algorithm identified brief (<2 GPS fixes) switch to a different behaviour, we further smoothed the data by merging any brief segments that occurred for < 4 minutes into the previous classified behaviour. We then defined behavioural 'bouts' in each trip as each consecutive trip segment of > 5 minutes in a single behaviour (i.e. a foraging bout was any segment of the trip classed as foraging that was at least 5 minutes in duration, as in Jones et al., 2018). HMM analysis was performed using the R package momentuHMM v. 1.4.3 (McClintock & Michelot 2018).

Selecting association thresholds

To ensure colony co-departures and co-returns reflected a biologically relevant association, we first defined a time-window of 3 minutes, a threshold that has been found to identify social co-departures (Jones *et al.* 2018). We then examined the difference in angle between both the temporally co-departing and co-returning pairs to identify temporally co-occurring incidents that also shared a direction of travel. From the distribution of the difference in travel angle we found that the majority of birds that co-departed or co-return within the 3-minute time window had a difference in angle below 25^{o}, indicating a shared heading. A smaller proportion of birds had large

difference in travel angle, which would suggest that although they depart/return the colony within the same 3-minute period, they do not appear to be associating. There was a noticeable break in the distribution of difference occurring at 50^{o}, as such we decided to set our threshold just below this cut-off at 45^{o} (Supplemental Figure 3.2).

To define co-commuting associations, we once again aimed to only retain biologically relevant co-occurrences. We therefore first selected the distance threshold of 1500m, as this distance is well within the visual range of gannets (Thiebault *et al.* 2014b). Additionally, when considering the distance covered by gannets during the sampling resolution (2 mins) we found on average gannets travel 1157 ± 1.7 m (mean ± SE), which falls just below our threshold (Supplemental Figure 3.3). Further, to avoid interactions in which individuals passed one another in different directions we looked at the distribution of difference in mean angle for pairs of individuals that were observed commuting within the selected distance threshold, and again found that for the majority of commute pairs of birds with 1500m differed in angle of travel by less than 50^{o} and therefore we used the same 45^{o} threshold as used for colony associations (Supplemental Figure 3.3). Similarly, to determine a threshold for duration we considered the distribution of duration that individuals spent within 1500m and found an initial peak in very short duration co-occurrences (< 5 mins) which indicate very temporary coordination of activity and thus we excluded these brief associations (Supplemental Figure 3.3). Additionally, these brief associations had significantly higher difference between angle of travel, indicating these brief associations were formed by birds travelling near one another but continuing in their own directions (pairs association <5 mins; mean difference in angle = 57.5^{o}, pairs associating >5 mins; mean difference in angle = 19.2^{o}, t-test; $t = 13.5$, $df = 321.7$, $p < 0.001$).

Similarly, to define foraging associations we expect individuals foraging together to be closer than our threshold used during commuting flight, which accounts for the fact that gannets move at a considerable speed while commuting. Although few studies have previously used GPS data to

attempt to define foraging associations in seabirds, some recent studies have considered individuals to be associating using thresholds from 500-2000m (Cook *et al.* 2017; Sutton *et al.* 2017; Brisson-Curadeau *et al.* 2018). We again considered the distances which gannets were observed to move between subsequent GPS fixes, and found that during foraging gannets travel on average 196 ± 0.55m (mean ± SE; Supplemental Figure 3.4). Furthermore, small forage fish are known to be found in shoals that can span large distances, for instance anchovy species have been found to occur in shoals ranging from 20-1600m in length (Pavlov & Kasumyan 2000). Thus, we selected a threshold of 500m for foraging associations, to encompass the distances moved by gannets during foraging and to account for the fact that a single prey patch may span a considerable distance. As in commuting associations, we again did not want to include brief associations which would indicate that co-occurring birds did not remain together at the foraging patch, thus we considered the distribution of time spent by foraging birds within 500m, and excluded the initial peak of short duration overlap under 5 minutes (Supplemental Figure 3.4).

Multi-layer community detection analysis

Multilayer community analysis assigns individuals to community clusters that can span from one to all of the layers of the multilayer network. As such, the maximum number of communities and individual can be assigned to corresponds to the maximum number of layers in which they appear (Finn *et al.* 2019). The communities identified depend on the connections between individuals within layers (as in single layer community analysis) as well as the connection between layers (De Domenico *et al.* 2015a). In multilayer InfoMap community analysis the coupling parameter between edges is controlled by the relax rate (spanning from 0 to 1), in which a relax rate of 0 indicates that layers are distinct and no communities can span more than one layer, and a relax rate of 1 indicates maximum coupling and the multi-layer is handled as an aggregate network (De Domenico *et al.* 2015a). As in Finn et al. (2019) we identified the minimum relax rate that produced a qualitatively different

community structure in comparison to the single layer InfoMap approach (Supplementary Figure 3.8).

Supplemental Table 3.1: Summary of individual foraging strategies. Number and sex of individuals specialising in each foraging strategy are given, as well as the total number of trips, median trip duration and median trips per individual. Note that individuals that specialised in one strategy were able to undertake trips of other types (up to 30% of trips, i.e. 9 females made at least one bay trip, but none were classified as bay specialists).

Foraging Strategy	Males	Females	Unknown	Total # of trips*	Median trip duration (hours)	Median trips per individual
Bay	13	0	0	249	4.1	21
Strait	16	34	1	474	14.8	9
Switch	19	2	0	262	9	13
Total	48	36	1	985	9.4	11

*total trips indicates the number of trips made by individuals classified into each foraging strategy. For switch individuals this was generally driven by individuals using a combination of bay and strait trips, rather than by making trips that used both the bay and the strait (only 3% of trips were classified as switch trips).

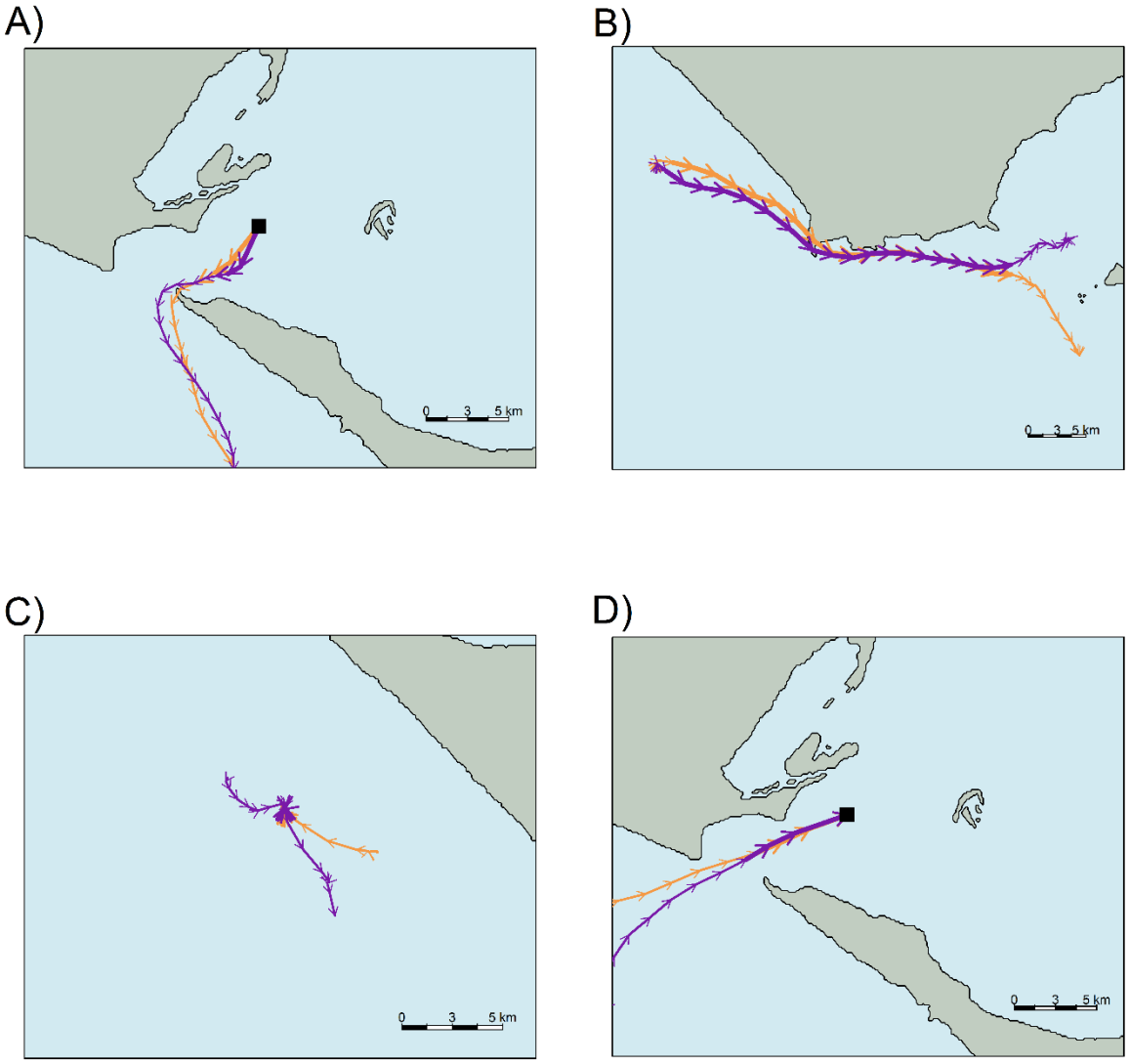
Supplemental Table 3.2: Comparison of social associations between network layers, indicating the consistency of dyadic associations across foraging contexts. Above the diagonal are the multilayer edge comparison of foraging states from gannet social associations in which the values represent the proportion of connections between individuals that are preserved between pairs of layers. Below the diagonal are the matrix correlations from pair-wise Mantel tests.

Layer	Departures	Commuting	Foraging	Returns
Departures		0.13	0.06	0.09
Commuting	0.13		0.17	0.12
Foraging	0.03	0.08		0.17
Returns	0.06	0.12	0.25	

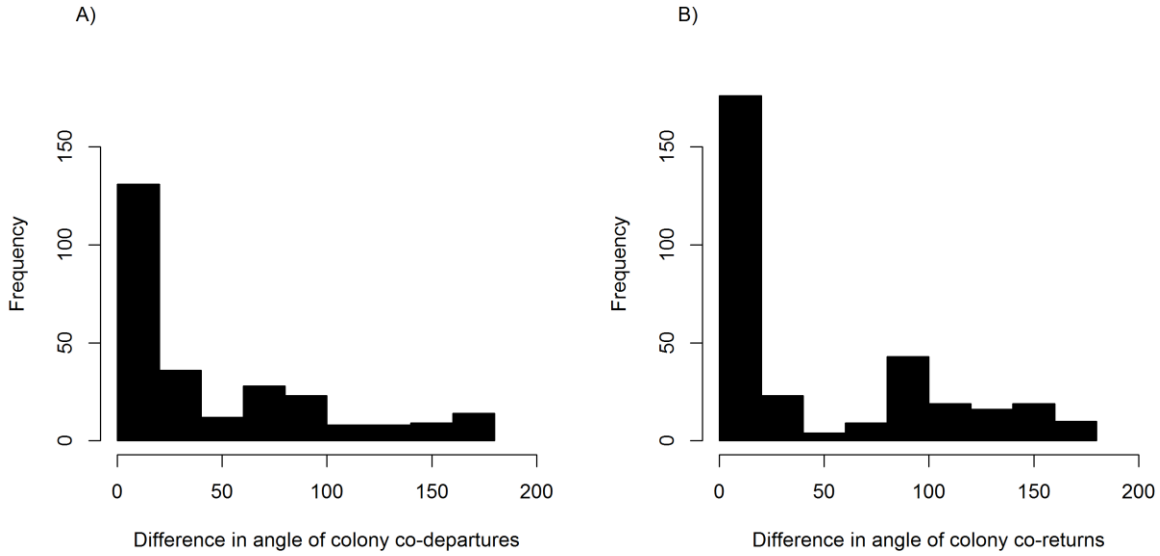
Supplemental Table 3.3: Comparison of social associations between network layers for non-bay individuals only, indicating the consistency of dyadic associations across foraging contexts. Above

the diagonal are the multilayer edge comparison of foraging states from gannet social associations in which the values represent the proportion of connections between individuals that are preserved between pairs of layers. Below the diagonal are the matrix correlations from pair-wise Mantel tests.

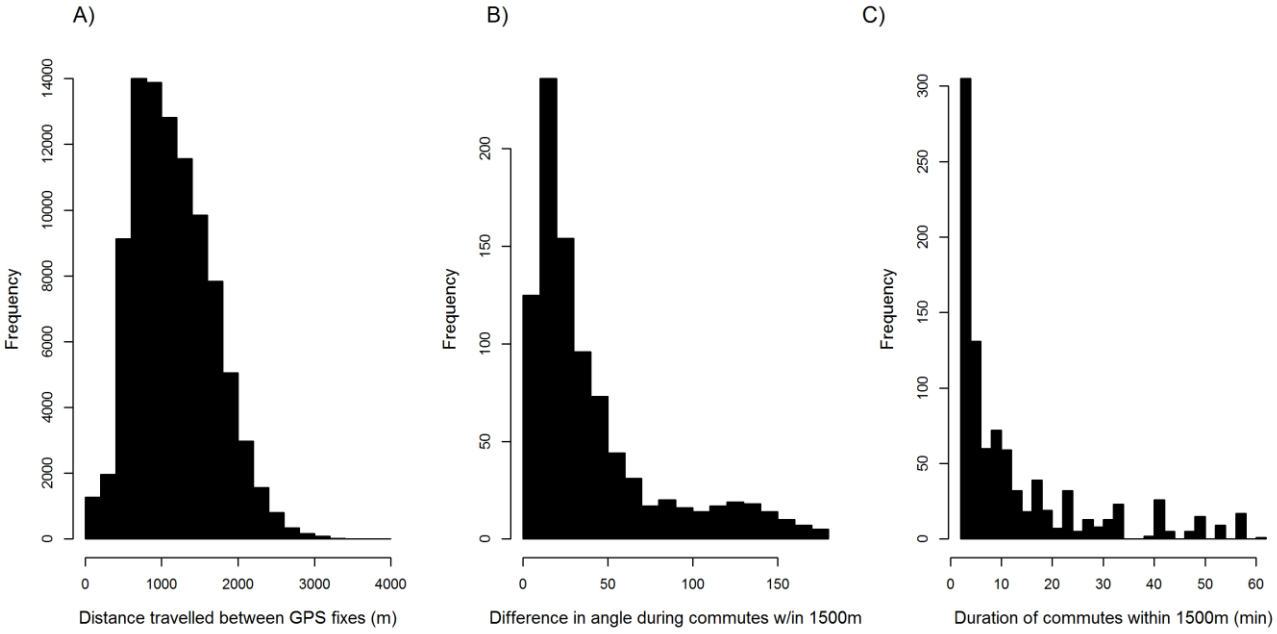
Layer	Departures	Commuting	Foraging	Returns
Departures		0.14	0.07	0.07
Commuting	0.12		0.23	0.12
Foraging	0.02	0.17		0.07
Returns	0.03	0.11	0.02	



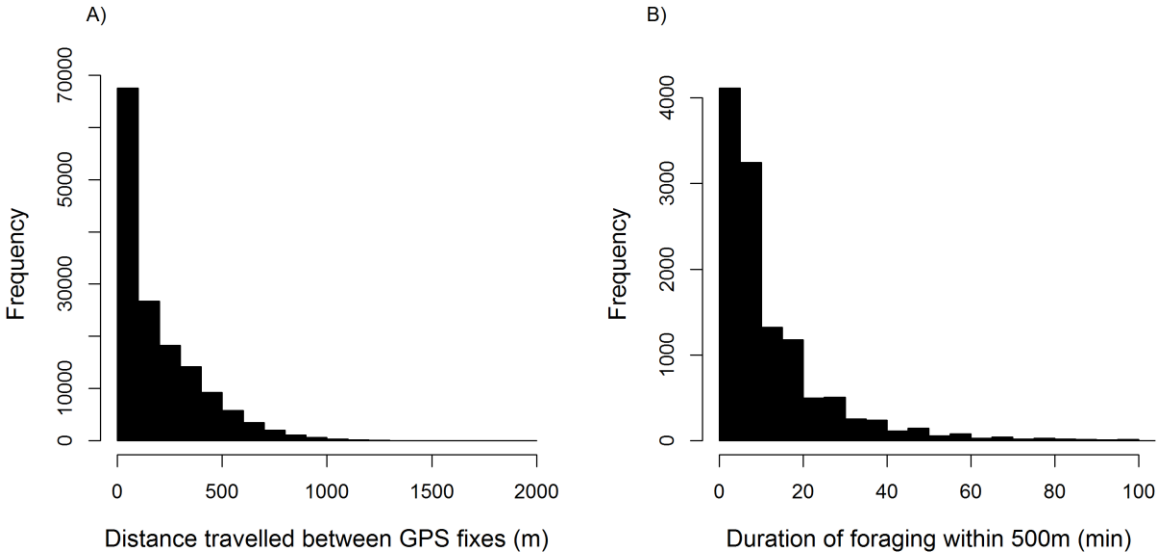
Supplemental Figure 3.1: Examples of associations as defined by distance, time and heading thresholds for each foraging state; A) Joint colony departure – within 3 minute time-window and difference in angle of travel <45°, B) Joint commuting – within 1500 m, difference in angle of travel <45° and duration of > 5 min, C) Joint foraging – within 500 m and duration > 5 min and D) Joint colony return – within 3 minute time-window and difference in angle of travel <45°. Arrows represent the direction of travel at each GPS fix (2 min resolution), the bolded portion of each track indicates the period of association; tracks are truncated for clarity, showing only the association and a period of 20 minutes before and/or after the association. In colony co-departures and colony co-returns the colony is indicated by a black square



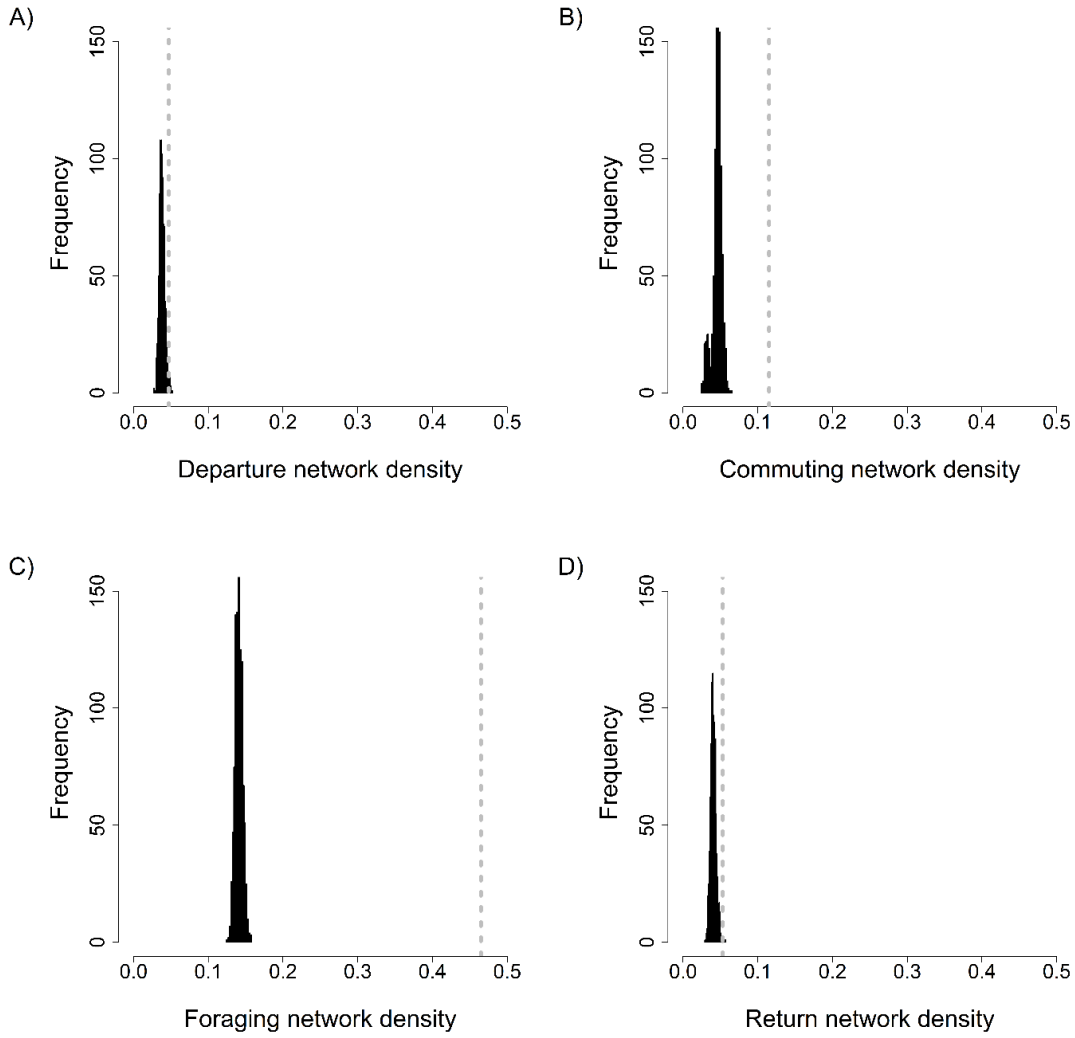
Supplemental Figure 3.2: Distribution of the difference in direction of travel (angle) between pairs of individuals that A) departed the colony and B) returned to the colony within 3 minutes of each of other.



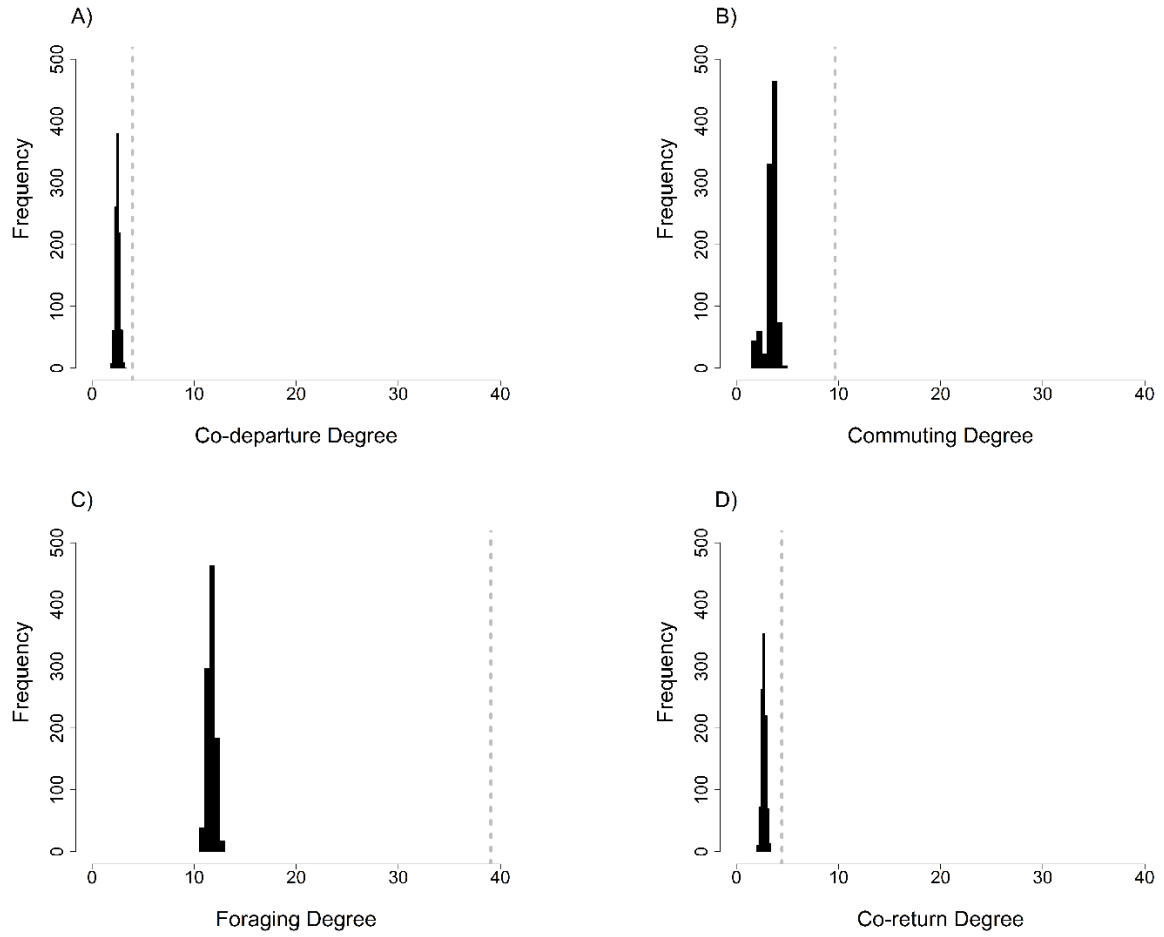
Supplemental Figure 3.3: Threshold selection for identifying co-commuting associations. A) The distribution of distance travelled between subsequent GPS fixes for points classified by the hidden-Markov model as commuting. B) Distribution of the mean difference in angle between pairs of birds that were commuting within 1500m of one another. C) The distribution of duration that birds spent commuting within 1500m.



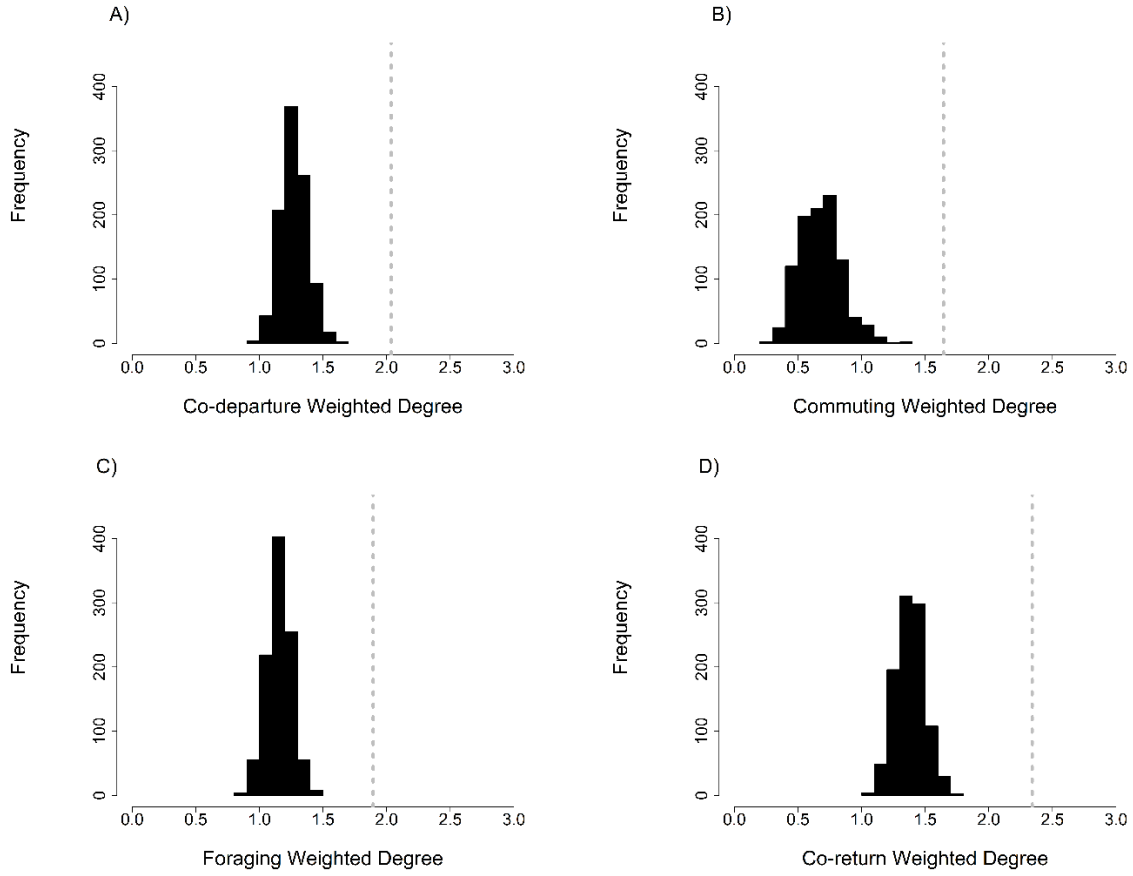
Supplemental Figure 3.4: Threshold selection for identifying co-foraging associations. A) The distribution of distance travelled between subsequent GPS fixes for points classified by the hidden-Markov model as foraging. B) The distribution of duration that birds spent foraging within 500m.



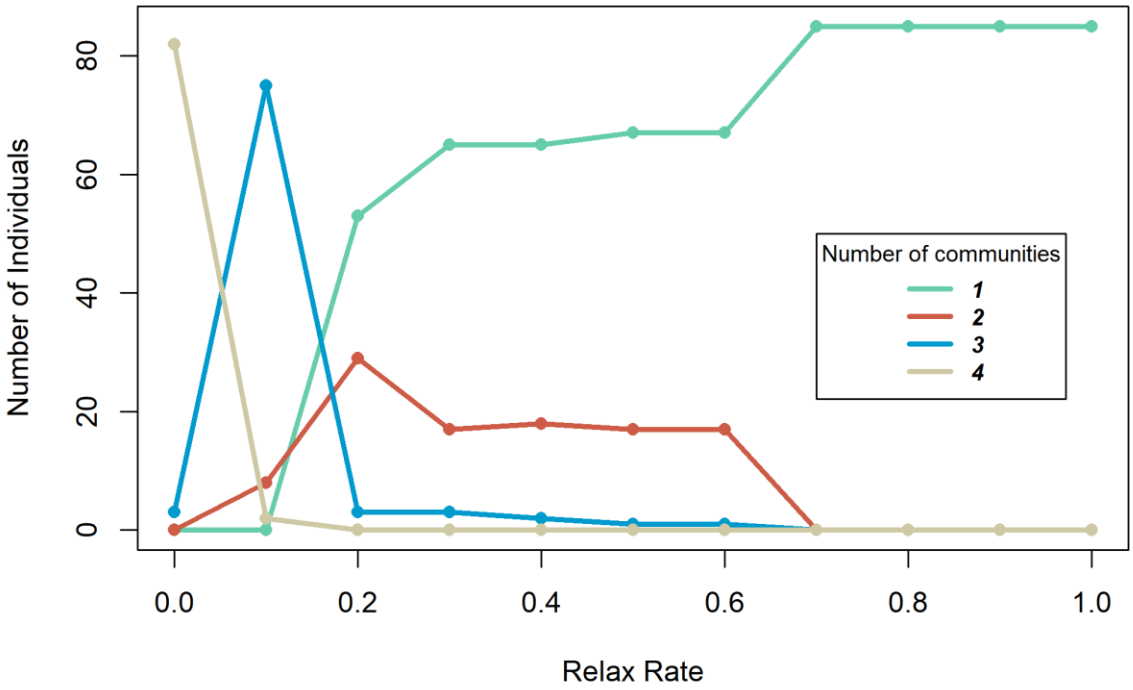
Supplemental Figure 3.5: Distribution of network density from 1000 data-steam permutations for A) colony co-departures network layer, B) commuting network layer, C) foraging network layer and D) colony co-returns network layer. Dashed lines indicates observed network density.



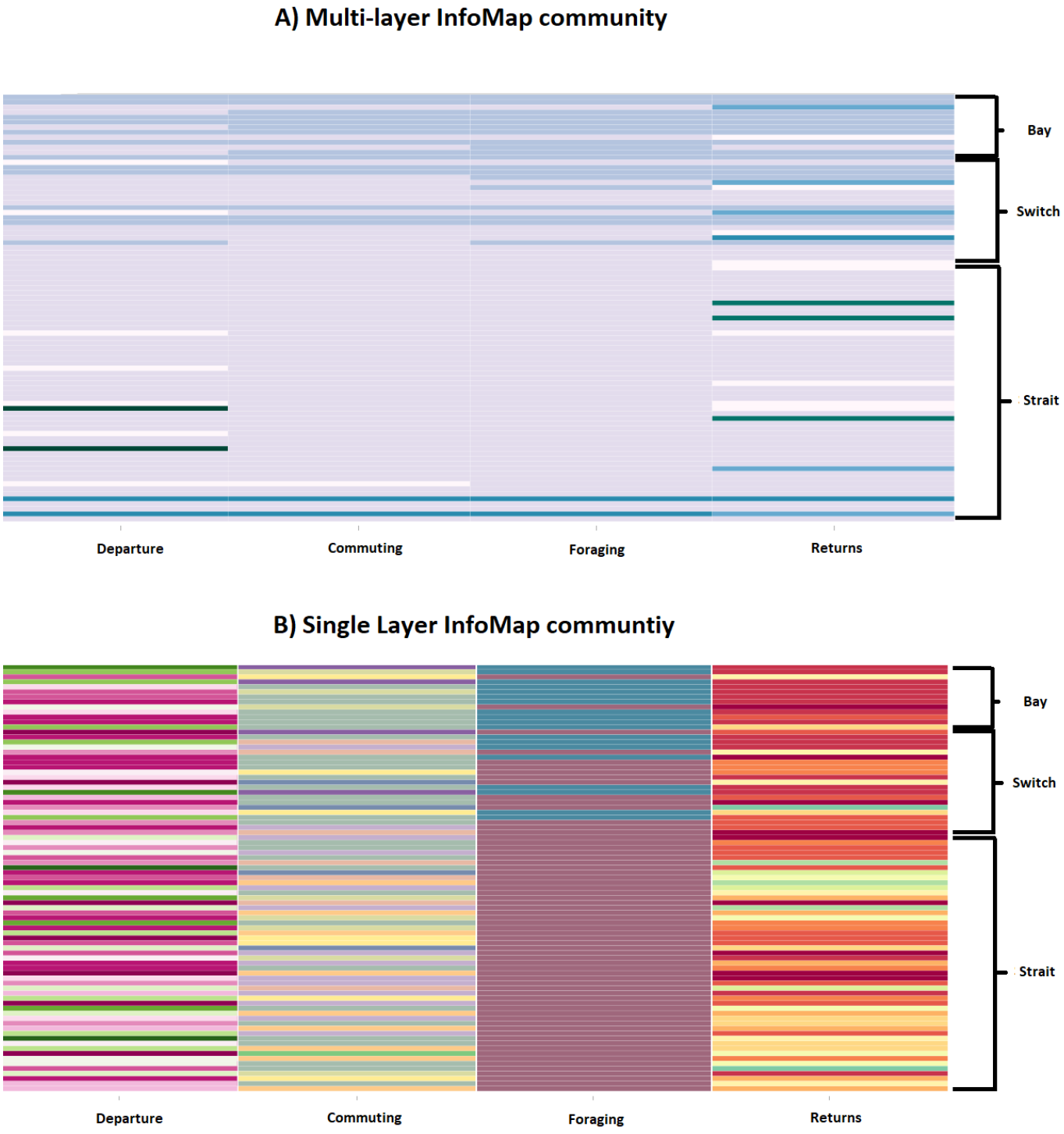
Supplemental Figure 3.6: Distribution of network degree, the number of associates, from 1000 data-steam permutations for A) colony co-departures network layer, B) commuting network layer, C) foraging network layer and D) colony co-returns network layer. Dashed lines indicates observed mean degree for each network layer respectively.



Supplemental Figure 3.7: Distribution of network weighted degree, a general metric of gregariousness, from 1000 data-steam permutations for A) colony co-departures network layer, B) commuting network layer, C) foraging network layer and D) colony co-returns network layer. Dashed lines indicates observed mean weighted degree for each network layer respectively.



Supplemental Figure 3.8: Number of communities in which individuals are members of as it varies across the mulit-layer relax rate. Individuals present in one community across all layers are shown in green, individuals classified into two communities are in red, those in three communities in blue and in four communities in tan. At a relax rate of 0.2, no individuals were classified in four different communities across the four layers and the majority of individuals were classified into one or two communities across the four layers.



Supplemental Figure 3.9: Community structure as assigned by A) Multi-layer InfoMap method and B) single layer InfoMap communities. Each row represents a single individual and each colour indicates a community. In the multi-layer, individuals assigned to the same community across multiple layers are represented as the same colour in two or more of the four network layers. In the single layer InfoMap, communities were restricted to within a single layer, thus communities in each layer are represented by different colour palettes. Individuals are also identified by spatial foraging strategy (bay, switch and strait) on the right hand side.

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Chapter 4

Flexibility in producer-scrounger behaviours during social foraging in a colonial seabird

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Abstract

When foraging in groups, animals have the opportunity to engage in social foraging strategies, in which individuals can exploit the search effort of others. Behaviours such as following other individuals and joining existing foraging groups or patches have been modelled as 'scrounging' behaviours, in which the following or joining individual acquires foraging information from one or more other individuals. However, to date there are few studies examining how both individual traits and experienced conditions combine to influence individual scrounging decisions within natural systems. Here we simultaneously record two forms of scrounging behaviours, following and patch joining, from 75% of breeding individuals from a colony of Australasian gannets (*Morus serrator*). We assess individual variation in scrounging behaviours, and determine how individuals adjust their scrounging decisions based on individual traits (sex and age) and external conditions. Our results show that individuals differ in their use of both following and patch joining decisions, but these differences were found to be flexible over time and not strongly driven by individual traits. Flexibility in both following and patch joining was found to be driven primarily by variation in conditions experienced across the foraging trip. Following was more frequent earlier in foraging trips, when energy reserves are predicted to be lowest and a small but reliable resource gain is required, whereas patch joining was found to occur more often later in foraging trips, which is expected to reflect an opportunistic return to a play-it safe scrounging strategy when reserves are nearly replenished. Both following and scrounging events tended to be longer in duration than producing events. Additionally, following and patch joining occurred more often closer to the colony, where scrounging opportunities are expected to be more abundant. Our results provide strong evidence that individuals engage in opportunistic use of scrounging behaviours, plastically adjusting their use of producer-scrounger strategies in response to temporal changes in the conditions experienced across a foraging trip.

Introduction

For animals that can forage in groups, individuals can acquire information about food resources both through personally sampling their environment as well as through a variety of social mechanisms (Dall *et al.* 2005). Individuals may gain information socially by copying or following potentially more knowledgeable individuals, or more simply individuals can be attracted to the foraging behaviours of others through the process of local enhancement (reviewed by Hoppitt & Laland 2013). As a result of using social information gained from following or joining behaviours, individuals are able to exploit the search efforts of other foragers (Giraldeau & Dubois 2008).

The use of such exploitative foraging strategies has often been modelled through the game theoretic context of the producer-scrounger (PS) model (Barnard & Sibly 1981; Vickery *et al.* 1991). Under the PS model, individuals can either search for new foraging opportunities (producing) or search for opportunities to join other foragers (scrounging), which leads to frequency-dependent payoffs associated with each strategy and thus is expected to produce a stable equilibrium of each strategy within a population (reviewed by Giraldeau & Caraco 2000; Giraldeau & Dubois 2008). The PS model of social foraging has often been used to study patch joining decisions (eg. Flynn & Giraldeau 2001) and kleptoparasitism (eg. Morand-Ferron *et al.* 2007), and has also been used to model information transfer through leading and following behaviour during the search stage of foraging (Barta & Giraldeau 2001), although to date there have been no studies explicitly evaluating scrounging behaviour during food search.

However, as in other models of social behaviour, our understanding of individual use of PS strategies is complicated by the prediction that individuals within a group will experience different costs and benefits from using social information to make foraging decisions (Ward & Webster 2016a). Thus if individual traits influence the costs and benefits received from PS strategies it may be expected that individuals express fixed differences in their use of producing and scrounging. For instance, inexperienced or young individuals may be less informed about foraging locations (Hoppitt & Laland

2013) and have been shown to be more likely to follow experienced or knowledgeable foragers (Harel et al. 2017; Palacios-Romo et al. 2019; Wakefield et al. 2019), which is expected to compensate for their relatively poorer foraging abilities and increase their foraging efficiency. Alternatively, in systems with strong linear dominance hierarchies due to differences in competitive ability between dominants and subordinates, payoffs from scrounger strategies are expected to be highest for dominant individuals (Barta & Giraldeau 1998). This has been found in previous work showing that older and dominant individuals are more likely to engage in scrounging behaviours that involve displacing subordinates (Bugnyar & Kotrschal 2002; Lendvai *et al.* 2006). Furthermore, sex differences in scrounging behaviours have been found in several systems, with females tending to scrounge more than males and to vary their scrounging tendencies in relation to their reproductive status (King *et al.* 2009; Aplin & Morand-Ferron 2017; Harten *et al.* 2018). These sex differences have been attributed to tolerance of scrounging by mates and due to differences in resource requirements depending on breeding state. Individual personality, or consistent individual differences in behaviours, has also been found to influence individual scrounging decisions. Scrounging has been suggested to be a variance reducing strategy, in which scrounging is expected to decrease the variance in food intake (moderate but consistent payoff) in comparison to producing (either high or low payoff)(Caraco & Giraldeau 1991; Koops & Giraldeau 1996), and as such risk-avoidance individuals may preferentially use scrounging behaviours. For example this risk-averse use of scrounging was found in a study of barnacle geese (*Branta leucopsis*), in which shy individuals were found to scrounge more often than bold individuals (Kurvers *et al.* 2010). However, in another study, no relationship was found between personality and scrounging (Aplin & Morand-Ferron 2017), although individuals were still found to express consistent use of PS strategies. Thus, it has been suggested that individuals may specialise in the use of producing and scrounging foraging strategies to minimise costs and maximise the benefits gained in relation to their individual traits.

In addition to variation in foraging outcomes experienced in relation to fixed traits, individuals may also experience fluctuating costs and benefits associated with producing and scrounging in relation

to the current experienced condition, such as the physical and social environment, current energy reserves or predation risk (Bugnyar & Kotrschal 2002; Lendvai *et al.* 2004). Thus, if the costs-benefit trade-off is primarily driven by these temporally variable factors, it is expected that any individual will benefit from flexibly adjusting their use of PS strategies to match the current conditions (Caraco & Giraldeau 1991). For instance, as scrounging is expected to reduce the variance in food uptake it is proposed that scrounging should be favoured when predation or starvation risk is high (Caraco & Giraldeau 1991; Koops & Giraldeau 1996). In a state-dependent dynamic model of producer-scrounger foraging, Barta & Giraldeau (2000) present that individual use of scrounging behaviour should vary based on time of day and energy reserves, to allow individuals to minimise starvation risk (i.e. scrounge when at low reserves early in the day) and maximise food intake (i.e. switch to higher payoff producing when initial risk of starvation is averted). There is some evidence from food deprivation in captive work, suggesting that energy reserves do influence scrounging frequency (Lendvai *et al.* 2004), but to our knowledge this model has not yet been tested in the wild using natural fluctuations in energy reserves. Patch quality has also been shown to influence PS foraging decisions with increased scrounging expected with increased patch density and richness (Koops & Giraldeau 1996; Beauchamp 2008). Furthermore, the payoffs of scrounging strategies are known to be frequency dependent in the short term, with the payoffs decreasing as the proportion of scroungers increases (Giraldeau & Caraco 2000; Giraldeau & Dubois 2008). Thus, individuals should alter their use of PS strategies in response to their social environment. For instance, previous work has demonstrated that while individuals express consistent foraging strategies in stable groups, these same individuals express flexibility in strategy when group composition changes (eg. Morand-Ferron *et al.* 2011). As such, individuals may be expected to express plasticity in their use of PS strategies, to best match their current level of motivation and in response to experienced environmental conditions.

Despite the long history of modelling and captive studies examining the factors influencing individual use of PS strategies there have been limited studies testing the relative importance of individual

traits and conditional influences on the use of PS strategies in free-ranging wild animals (but see Bugnyar & Kotrschal 2002; Morand-Ferron *et al.* 2007; King *et al.* 2009; Aplin & Morand-Ferron 2017). In particular, limited work has assessed how individuals may plastically adjust their scrounging behaviour in response to temporal changes in group composition, individual motivation and opportunity. In this study we aim to assess both the importance of individual traits (sex and age) on individual scrounging decisions as well as empirically testing the model presented by Barta & Giraldeau (2000) to determine how individual use of scrounging behaviour in Australasian gannets (*Morus serrator*; hereafter gannets) varies across a foraging trip. Although the original model presents a daily cycle common to most diurnal foragers, we posit that foraging trips over multiple days as seen in gannets represents the same cyclical pattern; a non-foraging period at the colony (night), initial departure from the colony (dawn), at-sea portion of the trip (day) and return to the colony (dusk).

Our study system also allows us to focus on multiple aspects of social foraging. Studies in the wild addressing the use of PS strategies have focussed only on patch joining and kleptoparasitic interactions with no studies to our knowledge investigating the factors influencing information scrounging during the search portion of a foraging trip. As gannets are central placed foragers during the breeding season, they are an ideal system in which to examine scrounging decisions during the search phase of foraging, as modelled by Barta & Giraldeau (2001), as all individuals must depart from a common location (the colony). In addition, seabird social groups represent a highly dynamic system fission-fusion system (Aureli *et al.* 2008) in which individuals express high flexibility in their social relationships (Jones et al submitted), and therefore represent an novel social system in which to test predictions developed from passerine focussed models.

This unique study system allows us to make a comprehensive assessment of scrounging behaviour in a free-ranging animal. Specifically, we examine the factors influencing scrounging in two social foraging contexts; 1) following behind a commuting individual during the search phase of the

foraging trip (following) and 2) joining actively foraging individuals (patch joining). We first assess individual variation in both following and patch joining decisions and determine whether these behaviours vary with individual traits (age and sex). We next examine individual flexibility expressed in individual use of producer-scrounger strategies by testing for repeatability of both following and patch joining decisions across time. We then explore the relationship between an individual's following and patch joining decisions, to assess how scrounging in a search context is related to scrounging in an active foraging context. Finally, we test the hypothesis that scrounging decisions will vary in response to changing conditions experienced across foraging trips. As measures of an individual's changing energy reserves we assess the effect of time through foraging trip, time of day, time between previous foraging/commuting events and duration of current foraging/commuting event. We additionally consider the effect of social environment on scrounging decisions by including the distance from the colony as individuals are expected to have increased opportunity to scrounge closer to the colony in higher forager densities.

Methods

Study system and behavioural classification

We collected at-sea forging data from adult gannets breeding at Pope's Eye colony located in Port Phillip Bay, Australia (38°16'42"S, 144°41'48"E), during chick rearing in January 2015. Gannets (n=100) were captured by hand on the nest and fitted with a GPS logger (igotU GT-600; 2 minute resolution. Mobile Action, Taiwan, 26.6 g, <1.7% of total body mass). Loggers were attached to central tail feathers by waterproof tape (Tesa 4651, Beiersdorf AG, Germany) to limit effects on hydrodynamics during plunge diving (Ropert-Coudert *et al.* 2009). Total handling time on logger deployment was < 6 minutes. We retrieved loggers 2-3 weeks after deployment and took morphometric measurements from individuals with a total handling time of < 15 minutes. GPS data was obtained from 85 loggers. All animal handling followed protocols approved by Deakin University

AEC (Approval B20-2013) and Department of Environment and Primary Industry (Victoria, Australia) Wildlife Research Permit 10006878.

To ensure equal time steps for behavioural classification, and simultaneous sampling for social analysis, GPS data was first interpolated to 1s intervals (adehabitatLT v. 0.3.23; Calenge 2006) and then resampled back to simultaneous 2-min time intervals. We then filtered the data to include only complete trips that departed from and returned to the colony (excluding a 500 m buffer around the colony to exclude temporary departures from colony due to disturbance as in Jones *et al.* 2018). To estimate the underlying behaviour of individuals during at-sea trips we used a hidden Markov model (Patterson *et al.* 2008) performed using the R package momentuHMM v. 1.4.3 (McClintock & Michelot 2018). This model estimates the underlying behaviour of individuals from the step length and turning angle between subsequently recorded GPS fixes. We used a gamma distribution for step length and a von Mises distribution for turning angle. Our model identified a three state HMM, with the three states corresponding to 1) fast directed flight (commuting), 2) moderate speed and high turning (foraging) and 3) low speed (resting on the water). We initially used the Viterbi algorithm to estimate the most likely behavioural states and then further smoothed the data, merging any brief switches in behaviour (< 4 minutes) into the previous behavioural state. We then defined a behavioural 'bout' as each consecutive trip segment that was > 5 minutes in duration spent in a single behaviour (as in Jones et al., 2018, and Jones et al. submitted).

Social associations during commuting and foraging were defined by spatio-temporal overlap in GPS data. A commuting association was defined as two or more individuals within 1500m for > 5 minutes, with a difference in angle of travel of < 45^{o}, indicating a shared direction of travel. Foraging associations were defined as two or more foraging individuals within 500 m for > 5 minutes (as in Jones et al. submitted). All individual commuting and foraging bouts that were identified as social (above) were considered together as a social commuting and social foraging events respectively.

As previous work in this study population has demonstrated that the spatial-temporal overlap of individuals foraging within Port Phillip bay does not occur at a rate significantly greater than is expected by chance under spatial null models (Jones et al. submitted), and individuals foraging within the bay forage predominantly on large solitary prey (Wells *et al.* 2016) we excluded all foraging bouts within the bay from analysis. We further excluded all GPS points collected at night (23:00 –04:00) as gannets are primarily diurnal foragers (Garthe *et al.* 2017) and overnight data consisted of primarily long segments of resting (rest bout duration at night: mean ± SE = 4.7 ± 0.04 hours).

Following and patch joining

To examine the use of scrounging behaviours we examined individual following (commuting) and patch joining (foraging) decisions, as measures of scrounging behaviour. During commuting, we identified the leading and following bird(s) at each time point during a social commuting event (Supplemental Figure 4.1) by calculating the linear distance between each individuals' GPS fix and the final position of the co-commute (defined as the midpoint between the final fix for each individual). An individual was then classified as a follower for a social commuting event, when found to be following for > 60% of the social association. For each social commuting event, we also defined the overall leader as any individual that spent >60% leading and we classified these individuals as the producer for that event. If an individual did not lead or follow in an event for over 60% of the event, we excluded the commute from the final analysis (14% of social commuting events). Individuals were also classified as a producer when commuting during any non-social commutes where another commuting individual was recorded within a minimum of 10km (within the visual range of gannets Thiebault *et al.* 2014) as this allowed us to consider additional non-social bouts that had potential for social association. For foraging bouts, a patch-joining event was defined as any bird joining an ongoing foraging event (Supplemental Figure 4.2). For all foraging bouts, the first individual to begin foraging was classified as the patch initiator, or producer for that event. Similarly, we also included

all non-social foraging events that occurred within 10km of another foraging bird as solo producing events.

Statistical analysis

As a subset of individuals (n=13) foraged predominately in Port Phillip Bay, some individuals participated in relatively few foraging and commuting events outside of the bay area. Thus to avoid influencing the results of all of the described analysis we excluded individuals with fewer than 15 foraging or commuting bouts outside the bay from all following analyses.

We first calculated the propensity of individuals to engage in scrounging behaviours, as the proportion of all potentially social commuting events that were follows and the proportion of all potentially social foraging events (as defined previously) that were joins, respectively for each trip. We next assessed how an individual's tendency to follow was related to their tendency to join patches. We constructed a binomial generalised linear mixed model (GLMM) with the proportion of foraging patches joined per trip as the response. We fitted the per trip proportion of following events as a fixed effect, and individual ID as a random effect. Next, to examine if propensity to scrounge varied with intrinsic traits of individuals we fitted separate binomial GLMMs to the per trip proportion of following events and the per trip proportion of foraging patches joined. Both models were fitted with the main effects age and sex and the interaction between age and sex as fixed effects and with individual ID included as a random effect. All GLMM models were fitted using lme4 v. 3.5.3 (Bates *et al.* 2015). Models were found to be overdispersed and an observation level random effect was included in each model. However, for the model of following the addition of an observation level random effect resulted in the model not converging, thus this model was retained without the observation level effect. Variable significance was assessed as variables in which the 95% CI around the estimate did not cross zero.

Repeatability of social strategy

To determine if individuals consistently employed scrounging strategies in both commuting (following) and foraging (patch joining) we calculated the adjusted repeatability (defined as the proportion of total variation explained by between-class variance; Nakagawa & Schielzeth 2010) of an individual's propensity to follow and join patches respectively. For both repeatability analysis, we fitted binary models with the response value of 0 for a scrounging event and 1 for a producing event during commuting and foraging respectively. In each model we fitted log distance from the colony, proportion through trip, hour of the day, log time between subsequent bouts of the same type (i.e. for foraging we fitted the time between previous and current foraging bout) and log duration of the current bout as fixed effects. All repeatability analysis was conducted using the RptR package v. 0.9.21 (Stoffel *et al.* 2017).

Factors influencing the use of scrounger behaviours

We next examined how extrinsic variables predicted scrounging decisions. For each commuting and foraging bout we scored a producing event as 1 and a scrounging event as 0. We then fitted binomial GLMM to commuting and foraging data separately with the following fixed effects: distance from the colony, proportion through trip, hour of the day, time between subsequent bouts of the same state (i.e. for foraging we fitted the time between previous and current foraging bout) and duration of the current bout. For distance from the colony, time between bouts, and duration of bouts we log transformed the variables and all fixed effect variables were mean standardised. In both models we fitted individual ID as a random effect. Variable significance was assessed as variables in which the 95% CI around the estimate did not cross zero. All statistical analysis was performed in R v.3.5.1 (R Core Team 2016).

Results

We recorded 73 individuals that made over 15 commuting bouts, for a total of 3296 commuting bouts of which 425 were social commuting events. When considering foraging behaviours we recorded 75 individuals with over 15 foraging bouts, for a total of 4765 foraging bouts of which 1623 were identified as social foraging events.

Individual variation in scrounging behaviour

Individuals varied in their propensity to use scrounger tactics during commuting and foraging. During foraging, the mean proportion of an individual's foraging bouts that were patch joining events was 0.28 (range: 0.04-0.58), while during commuting the mean proportion of an individual's commutes that were following events was 0.08 (range 0-0.25). An individual's propensity to scrounge during commuting and foraging were found to be positively correlated (Estimate = 0.29, 95% CI: 0.13-0.44, Figure 4.1).

Individual propensity to follow during commuting was found to not be influenced by the age or the sex of individuals or an interaction between the two factors (Table 4.1). During foraging, older individuals were found to have a higher propensity to join patches, but there was no effect of sex, or interaction between age and sex (Table 4.1).

Repeatability of producer/scrounger strategy

Individuals were found to show no repeatability in following behaviours (R = 0.006, 95% CI: 0-0.02). Similarly, individuals were not repeatable in their propensity to join foraging patches (R = 0.05, 95% CI: 0.02- 0.07). To ensure that the observed lack of repeatability was not driven by the high proportion of solo producing events during both commuting and foraging, we also calculated the repeatability including only social commuting and foraging events, and found similar results (Following: R = 0.07, 95% CI: 0-0.15 and Patch joining; R = 0.04, 95% CI: 0.01-0.08)

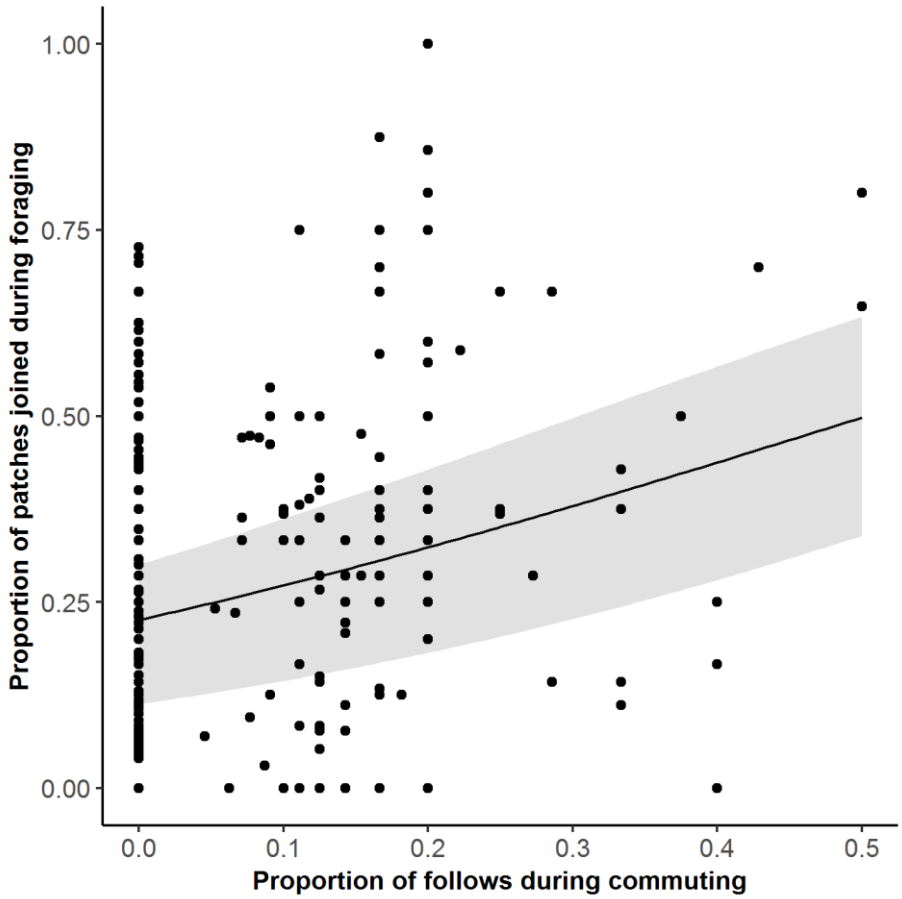


Figure 4.1 Estimated probability of individual per trip proportion of foraging patches joined given an individuals per trip proportion of follows during commuting. Plot shown with 95% confidence intervals. Based on binomial generalised linear models of patch joining and following.

Table 4.1: Model estimates and 95% confidence intervals for individual predictors of the proportion of commutes in which individuals follow and the proportion of forages in which individuals join. Significance is determined by confidence intervals not crossing zero, and significant terms are shown in bold.

Model parameter	Estimate	2.5% Confidence interval	97.5% Confidence interval
Following			
Intercept	**-2.55**	**-2.78**	**-2.35**
Sex_{male}	-0.02	-0.34	0.29
Age	0.12	-0.09	0.35
Age:Sex	-0.05	-0.39	0.27
Patch Joining			
Intercept	**-1.04**	**-1.31**	**-0.78**
Sex_{male}	-0.37	-0.77	0.04
Age	**0.28**	**0.013**	**0.55**
Age:Sex	-0.06	-0.47	0.33

Factors influencing use of scrounger tactic

When examining the factors related to the likelihood of an individual following during a commuting event, model estimates indicate that individuals are more likely to follow other commuting individuals when closer to the colony, earlier in their trip and earlier in the day. When following, individuals also spent longer in their commute, but there was no significant effect of the time between commuting events (Figure 4.2, Table 4.2). Similarly, for patch joining the model estimates indicate that patch joining occurred closer to the colony and later in the foraging trip, with no effect of time of day. Additionally, individuals were more likely to join when time between patches was short and joined patches were found to be longer in duration (Figure 4.2, Table 4.3).

Table 4.2: Model estimates, 95% confidence intervals and variable importance as determined by AIC_c weights, for predictors of following during a commuting bout. Significance is determined by confidence intervals not crossing zero, and significant predictors are shown in bold.

Model parameter	Estimate	2.5% Confidence interval	97.5% Confidence interval
Following			
Intercept	**3.20**	**2.97**	**3.47**
log(distance to colony)	**0.99**	**0.77**	**1.24**
Proportion through trip	**0.20**	**0.03**	**0.38**
Hour of day	**-0.17**	**-0.34**	**-0.002**
log(Time between commuting events)	0.04	-0.14	0.22
log(commute bout duration)	**-0.29**	**-0.47**	**-0.10**

Table 4.3: Model estimates, 95% confidence intervals and variable importance as determined by AIC_c weights, for predictors of patch joining during a foraging bout. Significance is determined by confidence intervals not crossing zero, and significant predictors are shown in bold.

Model parameter	Estimate	2.5% Confidence interval	97.5% Confidence interval
Patch Joining			
Intercept	**1.35**	**1.21**	**1.51**
log(distance to colony)	**0.88**	**0.78**	**0.98**
Proportion through trip	**-0.11**	**-0.18**	**-0.03**
Hour of day	0.04	-0.04	0.13
log(Time between foraging events)	**0.83**	**0.72**	**0.93**
log(Forage bout duration)	**-0.38**	**-0.47**	**-0.30**

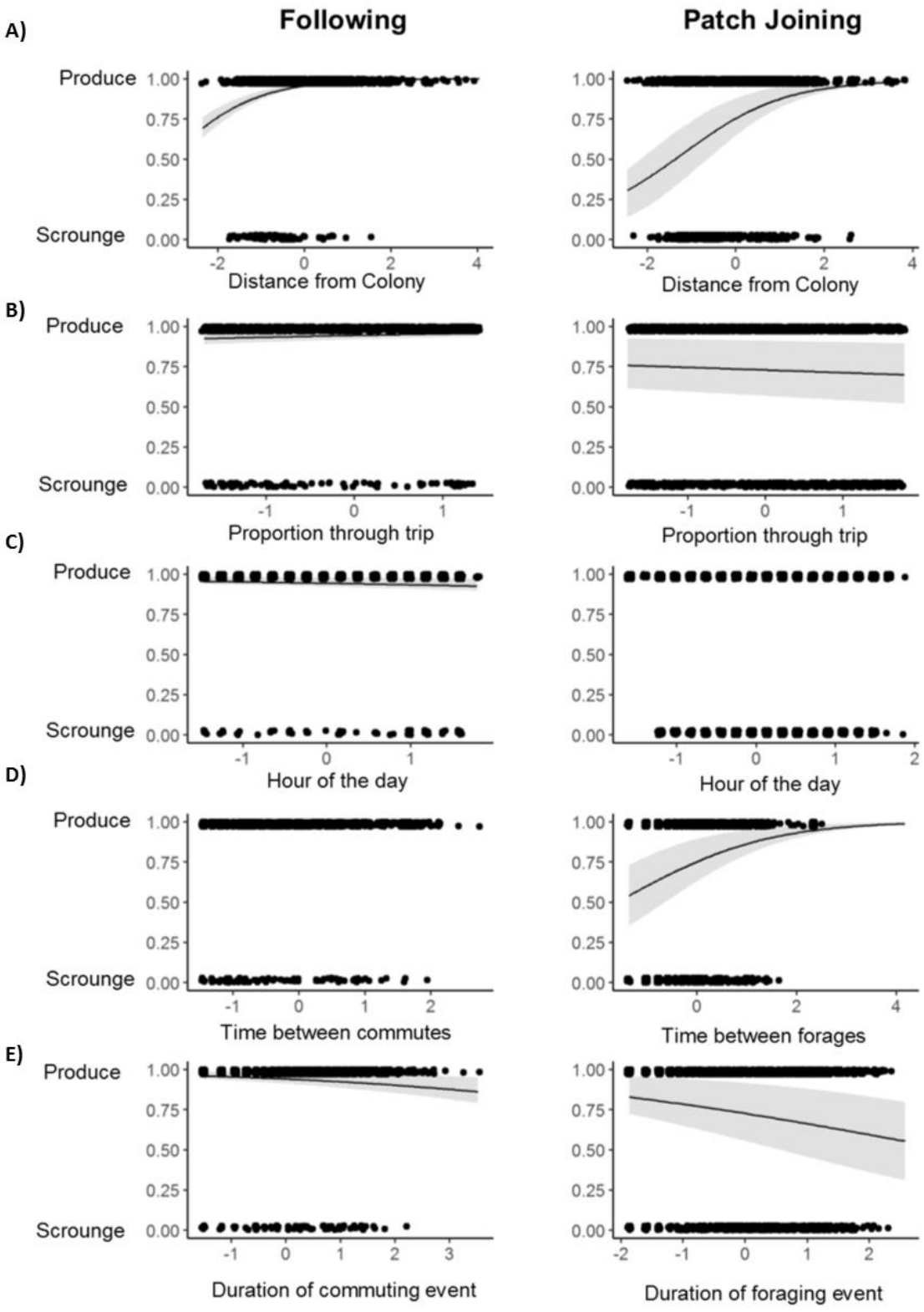


Figure 4.2 Estimated probability of individual producing or scrounging during commuting (following) and foraging (patch joining) for A) distance from the colony, B) proportion of time through trip, C) hour of the day, D) time between events and E) duration of event. All plots shown with 95% confidence intervals. Based on binomial generalised linear models of following and patch joining.

Discussion

In this study we provide a comprehensive assessment of the factors influencing producer-scrounger foraging strategies during both following and patch joining contexts in a wide-ranging central place forager. In doing so we provide a novel test of the dynamic state-dependent model presented by Barta & Giraldeau (2000). Our results demonstrate that in highly dynamic social groups, individual use of scrounging behaviours is highly flexible, varying in response to experienced conditions. Specifically, we found that individual tendency to scrounge during following was not repeatable across trips, and did not vary in relation to individual age or sex. Similarly, an individual's tendency to join foraging patches was not repeatable over time, and only age was found to influence probability to join, with older individuals joining foraging patches more frequently than younger individuals. However, we did find a positive relationship between an individual's propensity to follow and their propensity to join patches within trips. Both following and patch joining decisions were found to vary with conditions experienced on individual foraging trips. As predicted by the state-dependent foraging model, following occurred more frequently near the start of foraging trips when individuals are expected to have low energy reserves. Additionally following occurred more later in the day, which may reflect a response to decreased remaining foraging time before night and closer to the colony site, likely reflecting a higher availability of scrounging opportunities. Additionally, commutes in which an individual was a follower were longer in duration than commutes in which individuals lead or commute alone. For patch joining, individuals were found to join more frequently towards the end of foraging trips and closer to the colony. Joining events were also found to last longer and were found to occur sooner after a previous foraging event in comparison to producing events. Thus, our study provides strong evidence that in this system, temporally variable conditions are the main drivers of flexible use of PS strategies.

As individuals within a group experience different costs and benefits to sociality, individuals may express the use of social foraging strategies differently to maximise their foraging effort, based on

their individual traits (Barta & Giraldeau 1998; Beauchamp 2006). However, in our study, we found only an effect of age on the likelihood of individuals joining active foraging patches, with older individuals found to join patches at a higher rate. When scrounging involves displacement of the producing individual, previous studies have demonstrated that older and dominate individuals are more likely to engage in scrounging (Bugnyar & Kotrschal 2002; Lendvai *et al.* 2006). However, as multiple gannets can exploit the same food patch simultaneously and co-feeding has been shown to increase foraging rates (Thiebault *et al.* 2016), age differences are not expected to result from competitive displacement. Thus if group foraging is advantageous, increased patch joining in older individuals could be related to increased foraging experience, as individuals may learn to maximise their foraging efficiency by selectively choosing to dive in groups. In a recent study of northern gannets (*Morus bassanus*) it was demonstrated that juveniles are more likely to follow during commuting flights, and the authors present evidence that such following tendency was not explained by difference in flight mechanics, thus juvenile following may be related less experienced individuals following more knowledgeable adults (Wakefield et al. 2019). Thus, age differences between adults and juveniles may be more significant than those among adults, as the difference in experience is much greater between these stages than between differently aged adults, especially in long-lived species with extended juvenile period, such as the case in many seabirds. However, in the present study we were only able to follow breeding adults (all >4 years of age), and therefore were unable to detect age differences that may relate to juvenile individuals, even though they were likely to be foraging in the same environment.

For social foraging animals, individuals can scrounge from the foraging opportunities of other individuals through a variety of mechanisms, such as patch joining, kleptoparastism or food sharing (Giraldeau & Dubois 2008) and across different contexts such as during search or at the foraging patch. Although it has been proposed that information scrounging through following behaviours is a form of scrounging during the search phase of foraging (Barta & Giraldeau 2001), there have been no studies comparing scrounging behaviours across different portions of a foraging trip. Few studies

have previously compared different mechanisms of scrounging, with one study of scrounging behaviours in ravens (*Corvus corax*) demonstrating that individuals differed in the type of scrounging behaviour they engaged in, with older individuals tending to displace others whereas juveniles made more kleptoparsatism attempts (Bugnyar & Kotrschal 2002). In this study of ravens, scrounging mechanisms were also found to vary temporally, with displacement scrounging occurring most at the start of a feeding period and food-stealing and sharing becoming more common as food became depleted; however, these different scrounging behaviours all took place in the context of the food patch. Thus, to our knowledge, no studies have previously assessed scrounging decisions during both food search (following) and at the food patch (patch joining) together. As such, our results allow a novel examination of the relationship between individual scrounging decisions during two different scrounging contexts. Our findings indicate that although individuals were not repeatable in their tendency to scrounge within a context, individuals that are more likely to scrounge in one context are also more likely to scrounge in another. This result aligns with previous work on this population, which has demonstrated that individuals are consistent in their level of sociality across different foraging contexts (Jones et al. submitted), and supports the idea that individuals vary their scrounging in response to current state, as an individual's energy reserves may vary greatly between trips, but within a trip could lead to correlation in scrounging between search and forage.

In the producer-scrounger model of social foraging, benefits from the scrounger strategy are frequency-dependent, and as such it is predicated that the proportion of individuals playing each strategy will meet an evolutionarily stable strategy (Giraldeau & Caraco 2000; Giraldeau & Dubois 2008). Although several studies have demonstrated individual consistency in the use of PS strategies (i.e. Aplin & Morand-Ferron 2017; Harten et al. 2018) it has been shown that when group composition changes, individuals may alter their use of PS in response to the new group composition (Giraldeau & Lefebvre 1986; Morand-Ferron et al. 2011). Such flexibility in individual use of scrounging can help to maintain a stable level of producers and scroungers foraging at any given time (Mottley & Giraldeau 2000). Thus, it might be expected that in highly dynamic groups, such as

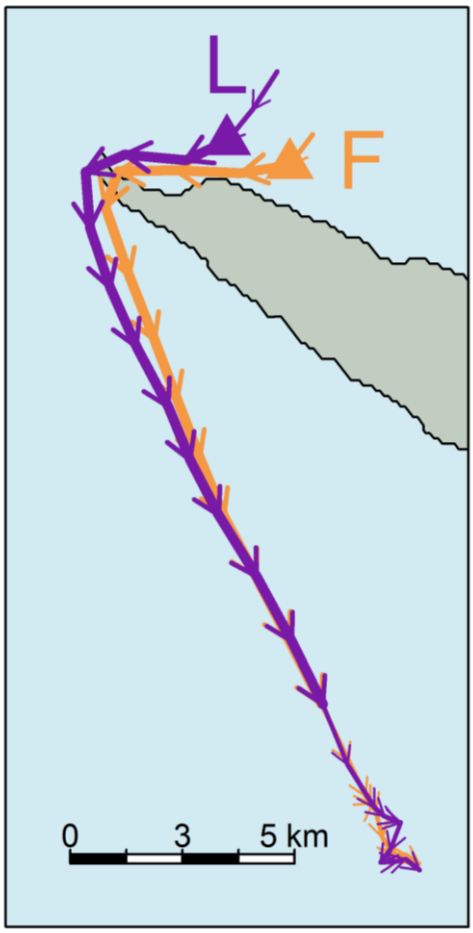
highly fission-fusion based social groups seen in foraging seabirds, individuals will be flexible in their use of PS strategies. Indeed, our results show that individuals were plastic over time in both following or patch joining decisions. Therefore, our data support the hypothesis that individuals flexibly express PS strategies to reflect their current need (i.e. energy reserves) and in respect with the current available opportunities (i.e. when there are few options to scrounge, individuals should produce).

When the costs and benefits experienced from scrounging vary in response to temporally changing conditions, it is expected that individuals will plastically adjust their use of producer-scrounger strategies to minimise costs invested and maximise the benefits gained. For instance, modelling work has highlighted the increased use of lower cost scrounger strategies during periods of highest risk for starvation, in the case of wintering passerines being first thing in the morning and during the pre-dusk period (Barta & Giraldeau 2000). In a similar fashion, our results show that individuals engaging in following behaviour more often at the start of foraging trips, which is expected to represent a period of time in which individuals are low on reserves having spent a prolonged period at the colony (mean ± SE: 9.0 ± 0.34 hours spent at colony between foraging trips). This may be particularly important during the chick rearing period in which individuals experience increased energy expenditures (Green *et al.* 2013; Dunn *et al.* 2018). Such following behaviour early in the trip could also be a result of individuals departing on a foraging trip after an extended period of colony attendance being uninformed as to current foraging locations, as relying on prior personal information can be less successful in temporally unpredictable environments (Deygout *et al.* 2010; Boyd *et al.* 2016). Thus, individuals initially may favour scrounging to quickly and reliably locate a foraging patch before switching to the more risk-prone producing (Caraco & Giraldeau 1991; Koops & Giraldeau 1996). Additionally, we found that patch joining increased later in foraging trips, which could suggest that individuals opportunistically take advantage of any encountered foraging patches during the return portion of the foraging trip. Late-trip scrounging is expected when individuals have reached or nearly reached their required resource intake from the foraging trip and thus switch back

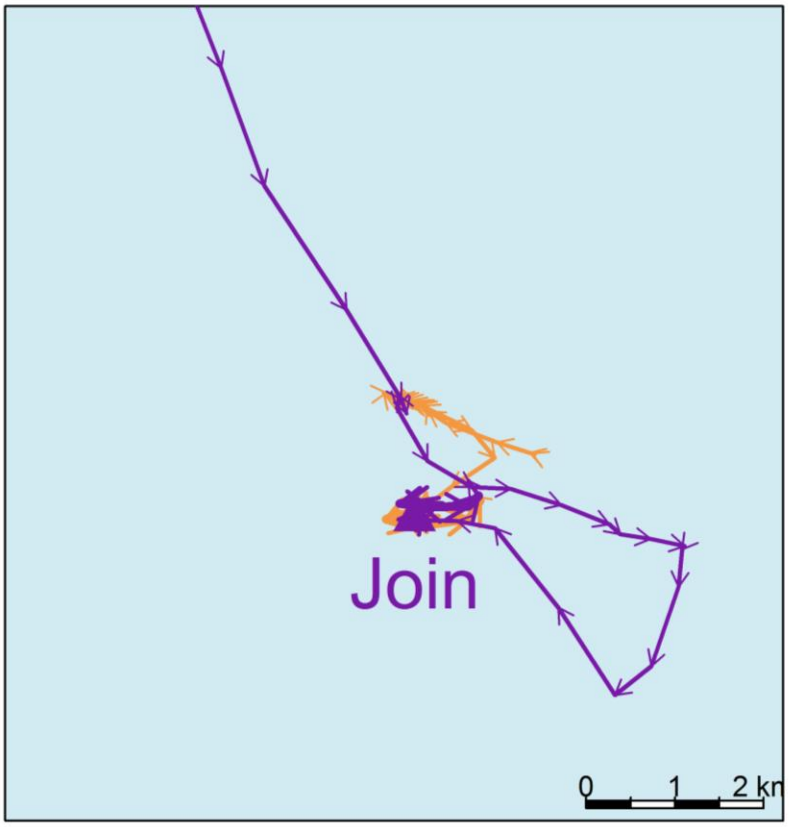
to the risk-averse strategy of scrounging to obtain a smaller but more reliable foraging outcome (Barta & Giraldeau 2000). Both following and patch joining was found to occur at a higher rate closer to the colony. As such, it seems that the relationship between scrounging and distance from the colony could be related to opportunity, as individuals are expected to preferentially forage at the minimum available distance from the colony (Dukas & Edelstein-Keshet 1998) and foraging intensity is expected to be highest in a 'halo' directly around the colony (Ashmole 1963). Thus, individuals should encounter more opportunity to engage in exploitative foraging in areas with higher forager density close to the colony site. Together, our results of plasticity in the use of scrounging across a foraging trip match the predictions of the daily pattern of social foraging modelled by Barta & Giraldeau (2000), demonstrating that individuals alter their use of PS strategies in response to predictable patterns in foraging cycles.

Our study simultaneously tracked the following and patch joining decisions of the majority of breeding individuals from a small colony of Australasian gannets, which are a wide-ranging central place forager. Our findings demonstrate that in a highly dynamic fission-fusion system, individuals express flexibility in scrounging decisions. Individuals adjust their use of both following and patch joining across the trip in a manner expected to reflect temporal changes in energy reserves (proportion of time through trip, time of day, and time since last forage) as well as in response to scrounging opportunity (distance from the colony). Interestingly, we found a positive relationship between an individual's patch joining and following tendencies which could suggest that although we did not detect individual consistency within either strategy, within a given trip individuals express consistent scrounging patterns across contexts. To further our understanding of the scrounging decisions of individuals it would be valuable be able to measure the energetic benefits gained from scrounging in different contexts and under various foraging conditions.

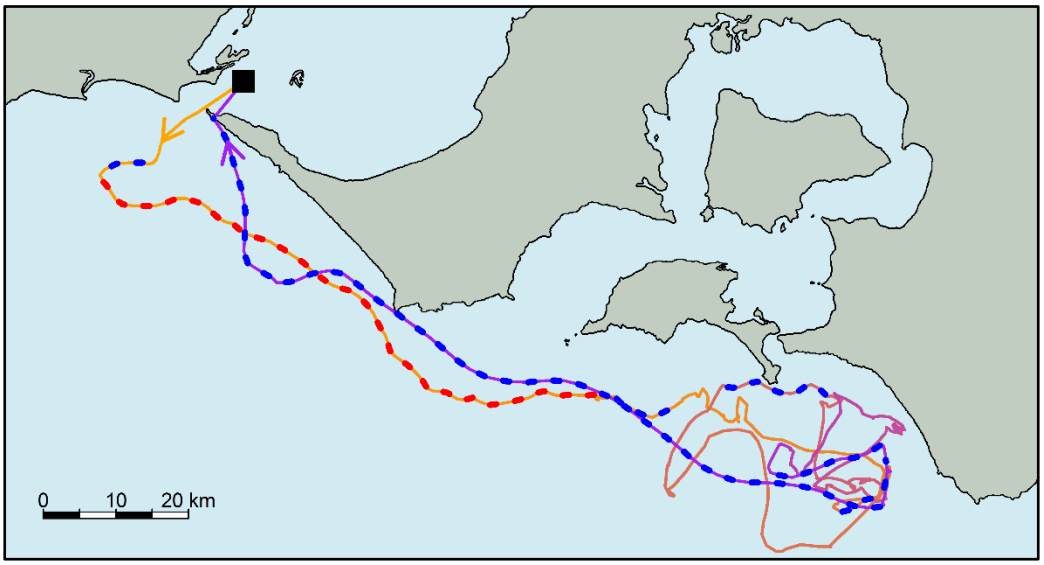
Supplemental Materials



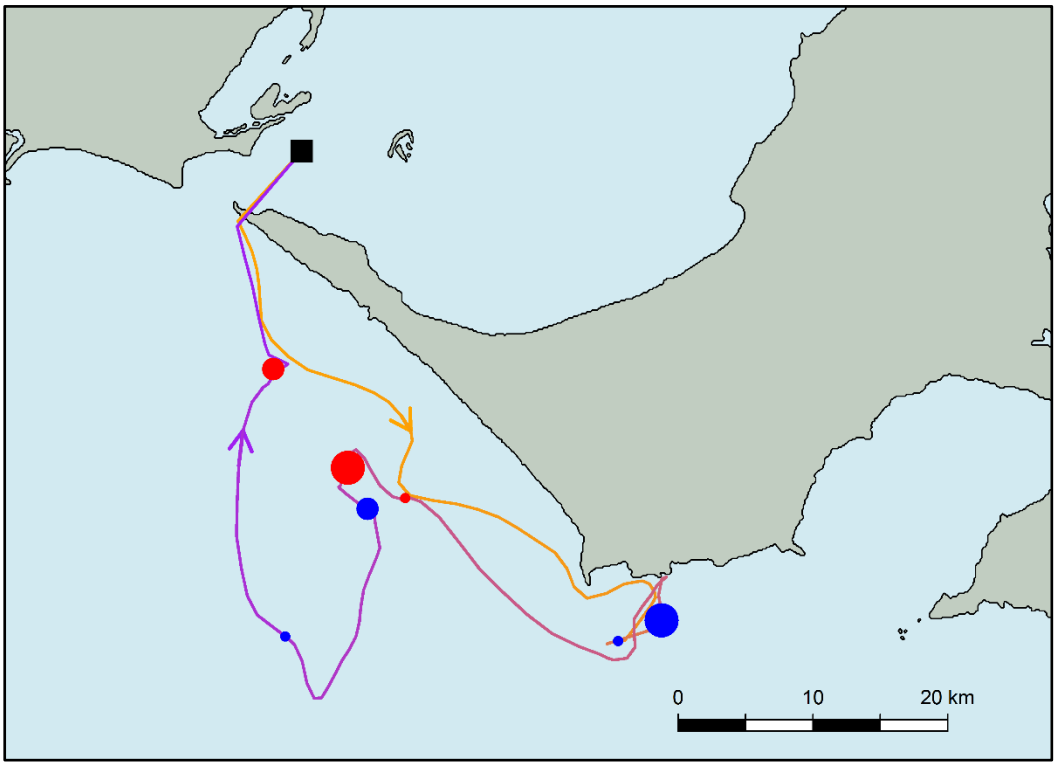
Supplemental Figure 4.1: Example of social commuting event with direction of travel indicated by arrows. Leading individual is shown in purple, with the initial GPS point in the social commute labelled “L”. Following individual is shown in orange with initial GPS point in the social commute labelled “F”.



Supplemental Figure 4.2: Example of social foraging event with direction of travel indicated by arrows. Joining individual is shown in purple, with the GPS point indicating the patch joining event (the point the individual switched from commuting to foraging) labelled "Join". The producing individual is shown in orange.



Supplemental Figure 4.3: Example of individual foraging trip with direction of travel indicated by arrows. Commuting segments marked with dashed lines, producing events shown in blue and scrounging events in red. Colony location is marked with a black square.



Supplemental Figure 4.4: Example of individual foraging trip with direction of travel indicated by arrows. Foraging patches marked with circles, producing events shown in blue and scrounging events in red. Circle size represents duration of foraging event. Colony location is marked with a black square.

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Chapter 5
General Discussion

Sociality in animals is expected to have evolved when there is a net positive trade-off between the potential benefits of conspecific and/or heterospecific association (i.e. predation dilution, cooperative behaviours, social information) and the increased costs associated with group living (i.e. competition, disease exposure) (Krause & Ruxton 2005; Beauchamp 2014b; Ward & Webster 2016). Coloniality represents one extreme of animal societies, and although the evolutionary origins of colonial living are still debated (Danchin & Wagner 1997; Danchin et al. 2008), there is strong evidence that access to social information is a key driver maintaining such complex social systems (Boulinier & Danchin 1997; Danchin et al. 2004; Dall et al. 2005; Valone 2007; Evans et al. 2016). For colonial seabirds, social foraging, particularly through increased access to socially available information, has long been proposed as a key benefit to the dense breeding aggregations typical of these species (Shealer 2001). However, our understanding of the intrinsic and extrinsic factors driving individual social foraging decisions in colonial seabirds has been limited by the difficulty of studying behaviour of such long ranging species. In particular, important social foraging associations occur at-sea and are thus difficult to observe directly. This thesis takes advantage of technological developments that have made it possible to remotely record animal behaviours at resolutions relevant to social processes and obtain sufficient coverage of individuals to accurately assess social associations (Krause et al. 2013). In this chapter, I will summarise the key findings of this thesis in the context of social foraging processes including information transmission, local enhancement and exploitative foraging strategies. In particular, I will address how these social process are critical to colonial living seabirds, how this work further informs the broader study of social foraging and develops our understanding of how intrinsic and extrinsic factors drive important individual variation in social behaviours. Lastly, I highlight future research directions that will combine increasing advancements and availability of bio-logging technology with environmental variables to begin to address outstanding questions for colonial social foragers.

Key Findings

The overall aim of this thesis was to further our understanding of social foraging behaviours across multiple contexts in colonial breeding species. Specifically, I sought to address the lack of research connecting social associations across different stages of foraging in wide-ranging foragers and to improve our understanding of the underlying factors driving individual differences in sociality and social foraging decisions.

To test the hypothesis that the colony location acts as a centre for information transmission, it is vital to observe not only behaviour at the colony, but also to assess the response of individuals to colony-based information. In **Chapter 2,** I assess individuals departing the colony together, and link these colony associations to at-sea foraging behaviours. Individuals that co-depart the colony were found to share more similar initial foraging locations, highlighting that departing individuals at the colony may provide information accessible to other foragers. Next, I conducted a novel spatial-temporal analysis to identify periods of social association between individuals in **Chapter 3.** This work builds on analysis techniques (Hidden Markov Models) used to infer underlying behavioural states from bio-logging data. Using these underlying states, I was able to identify periods of spatial-temporal overlap between individuals co-occurring in the same behavioural state. From this data, I applied recently developed multi-layer social network analysis and spatially explicit null models to examine how individual sociality is expressed across different stages within foraging trips. I tested the hypothesis that social associations are influenced by both spatial (foraging location) and temporal (foraging state within a trip) contexts. I demonstrate that individuals express consistency in their social tendency, but a high degree of flexibility in their social associations. Furthermore, I show that sociality during colony co-departure and foraging is dependent on habitat occupied, with social associations only forming more often than expected by chance in habitats previously found to have less predictable patchy prey resources. Finally, In **Chapter 4** I empirically test a state-dependent dynamic model of the producer-scrounger foraging game presented by Barta & Giraldeau (2000). In

this chapter, I demonstrate that individuals flexibly adjust their use of exploitive foraging tactics in two contexts (search and foraging) in response to changing conditions experienced across the pattern of a foraging trip. In summary, it is clear that individuals within this population exhibit social foraging behaviours across multiple contexts, and opportunistically engage in social associations that are expected to maximise the benefits available from group foraging. These findings help us to understand more about the complex factors underpinning the consequences of sociality, particularly for colonial species that are expected to experience intense costs and benefits from social living.

Social foraging in seabirds

During foraging, individuals seek to maximise energy gain while minimising the costs of foraging (Stephens *et al.* 2007). Foraging costs for seabirds that travel over large distances to locate food in variable marine habitats are high (Weimerskirch 2007) particularly during the breeding season when individuals must provision offspring as well as themselves (Green et al. 2013; Dunn et al. 2018). For plunge diving gannets specifically, each individual foraging dive carries significant costs, forcing individuals to minimise their diving attempts (Green et al. 2009). Therefore, lower cost social information may be favoured over more costly personal exploration (Kendal et al. 2005; Hoppitt & Laland 2013).Throughout this work, I present strong evidence of social associations across a variety of foraging contexts (**Chapter 2-4**), highlighting the importance of social associations during foraging to Australasian gannets. However, to fully understand the cost-benefit trade-off of group foraging in seabirds, future work focussing on identifying the energetic gains between social foraging and solo foraging would be required. Some previous work has focussed on how foraging in groups can decrease search time to locate a food patch (Valone 1989), providing evidence that sociality during the search for prey patches could reduce energy expenditure in flight. In addition to the search portion of a foraging trip, foraging in groups can also influence the costs and profitability of prey items captured. In a recent study including the Pope's Eye gannet colony, capture success was found to be lower in solo foraging events, while lower prey profitability was found in multi-species foraging

groups (Cansse *et al.* 2020). Therefore, future work combining the total costs of both the search and capture phases of foraging, as well as accounting for the profitability of prey items is needed to fully quantify the potential benefits of social foraging in comparison with solo foraging.

The information centre hypothesis (Ward & Zahavi 1973) and the recruitment centre hypothesis (Richner & Heeb 1995) both posit that colonies and roosts may act as a centre for the transmission of foraging information and/or the active recruitment of conspecifics. However, the requirements of active signalling of foraging success and suggestions of group selection have resulted in these hypotheses being difficult to validate. At seabird colonies, information such as the direction of departure or return, may be difficult to conceal (Valone 1989), thus it is likely that individuals may take advantage of unintentional conspecific cues. While the information centre and recruitment centre hypotheses initially focussed on direct departures from colony or roost site, seabirds are known to congregate in the waters around their colony to bathe and preen immediately prior to, or on the return from, foraging trips (Burger 1997). This behaviour is generally referred to as 'splash-down' or 'rafting' and has been found to occur in close proximity to the colony (i.e. <600m, Burger 1997; <2km, Carter *et al.* 2016). There has been considerable interest in the purpose of these rafts with several studies suggesting that information transfer could occur in such rafts rather than at the colony site (Burger 1997; Weimerskirch *et al.* 2010; Machovsky-Capuska *et al.* 2013; Evans *et al.* 2015). This may be particularly important for burrowing or other spatially segregated colonies, in which individuals may be unable to assess the direction of departing and returning conspecifics from their nest location. Additionally, in many cases, birds in flight immediately around the colony often return to land on the colony, further confounding any attempt to match departures directly from the colony (Burger 1997), which has led to the idea that seabirds may use near-colony raft as a site of coordination for departing individuals. In particular, Weimerskirch *et al.* (2010), demonstrated that Guanay cormorants (*Phalacrocorax bougainvillii*) adjust the positioning of rafts to match the direction of large returning groups, providing a 'compass' for departing individuals. However, in another study on the rafting behaviour of Northern gannets (*Morus bassanus*) the authors' found no

evidence that joining rafts influencing foraging trip metrics, despite a majority of individuals joining rafts upon departure from the colony (Carter *et al.* 2016), which suggests that individuals do not receive a foraging benefit from participating in rafts. Gannets from the Pope's Eye colony studied in this work are known to raft within a very short distance from the colony (<500m, JPYA personal observation), and the small colony size allows individuals unobstructed view of conspecifics departing directly from the colony and from any nearby rafts. Thus, for the analysis presented here, I considered colony departures as movement beyond a 500 m buffer around the colony, which accounted for both direct colony departures and departures from near-colony rafts which are expected to be equivalent in this colony. For colonies in which the view of departing and returning individuals is restricted, it is likely that focussing on near-colony rafting behaviour, when present, will provide a better measure of potential social information use.

In this thesis, I took advantage of a naturally occurring small colony to concurrently track 85% of the breeding adults. The high proportion of individuals included in the study allowed for a thorough analysis of social associations. However, the use and benefits of social information may be higher as group size increases (King & Cowlishaw 2007), thus it is also important to understand how social behaviours may differ in large colonies. Indeed, previous work on a small colony has suggested the lack of any apparent information centre effect may be related to small colony size (Elliott *et al.* 2009). Studying the use of social information in large colonies is impeded by the difficulty of simultaneously tracking a large enough proportion of the colony to detect social associations. Although social associations of concurrently tracked individuals have been identified in samples covering a much lower proportion of the colony (for example: 20% of active foragers; Berlincourt & Arnould 2014, <1% of active foragers Cook *et al.* 2017), these studies result in a very small number of recorded associations that preclude examining individual differences in social behaviours. Therefore, the work in this thesis allows a comprehensive look at individual variation in sociality in a small colony, and provides a solid foundation to begin addressing sociality in large colonies. As social information is expected to be of greater reliability in larger groups (King & Cowlishaw 2007)

individual use of social information may be expected to be more prevalent in large colonies (Boyd *et al.* 2016). On the other hand, studies of large seabird colonies have also highlighted the significant impacts of interference competition between individuals using the same foraging areas (Lewis *et al.* 2001). Increased competition could result in the avoidance of social foraging, or the use of social information as a way to reduce the high competition costs that may be unavoidable for very dense colonies. The method of foraging a seabird species employs may also have a significant impact on the prevalence and benefits of social foraging behaviours. For instance, plunge diving gannets making successive dives in groups are known to have increased capture success (Thiebault *et al.* 2016). In other seabird species, such as surface-feeding kittiwakes, group foraging benefits may not exist or may not counter the costs from competition (Ainley *et al.* 2003). Future comparative work assessing the use of social foraging behaviours would be needed to understand the effects of different colony sizes and foraging methods on social foraging in seabirds.

Additionally, although beyond the scope of this thesis, future work into social foraging in seabirds should take into account foraging associations between individuals from additional colonies and heterospecific foraging groups, as seabirds are frequently observed foraging in mixed flocks and in close association with other marine predators (Jaquemet *et al.* 2005; Vaughn *et al.* 2010; Bairos-Novak *et al.* 2015). Although non-colony members and heterospecifics are unable to provide foraging information at the colony, they are still available to provide information via local enhancement. Due to the difficulty in simultaneously tracking multiple species, bird-borne cameras (as in Yoda *et al.* 2011; Votier *et al.* 2013; Thiebault *et al.* 2014) may be particularly useful for understanding the nature of heterospecific interactions, especially as the technology becomes smaller and more available. Such heterospecific associations may be of significant importance as heterospecific information has been shown to be of potentially equal value when compared with conspecific information (Seppänen *et al.* 2007). Indeed, heterospecific foraging cues may be particularly important in the case of small colonies such as the one at Pope's Eye which may have fewer opportunities for conspecific associations. This has been suggested by previous works which

demonstrate decreased social foraging with low forager density (Buckley 1997; Grünbaum & Veit 2003; Weimerskirch *et al.* 2010; Boyd *et al.* 2016).

Implications for other colonial and social foragers

Social foraging behaviours are thought to be of particular importance to marine-foraging seabirds (Shealer 2001), as social information has been demonstrated to be of greater value in patchy and ephemeral environments (Pöysä 1992; Beauchamp et al. 1997), and when prey is cryptic or difficult to locate (Barrette & Giraldeau 2006), both of which are typical in foraging seabirds (Weimerskirch 2007). Similar patchy environments are often exploited by colonial breeding and roosting species in terrestrial habitats. In the case of colonial roosts, foraging information has been suggested to have a direct effect on the formation of such roosts, as individuals are not constrained to return to these roosting sites in the same way that breeders must return to the colony to provision their offspring (Evans *et al.* 2016). For example, in models based on common ravens (*Corvus corax*) foraging from colonial roost sites it has been demonstrated that individuals should search individually and return to the roost and recruit other individuals to large but ephemeral food patches (Dall 2002; Dall & Wright 2009). Many insectivorous species also target highly ephemeral prey patches and have also been shown to forage in groups at a rate higher than expected by chance (as in Dechmann *et al.* 2010). Additionally, uninformed individuals from colonial roosting sites have been shown to follow informed individuals from the roost site to previously exploited food patches (evening bats (*Nycticeius humeralis),* Wilkinson 1992; Eurasian griffon vulture (*Gyps fulvus*), Harel *et al.* 2017). The findings from this thesis contributes to the body of knowledge aiming to understand the prevalence and importance of social foraging behaviours across the diversity of colonial systems.

In this thesis, I present strong evidence that gannets presented consistency in overall gregariousness but high flexibility in social associates (**Chapter 3**). However in many social systems individuals maintain long-term cohesive social groups, and thus specific social associations are expected to have a significant impact on the social foraging behaviours of individuals. For instance in many social

systems, dominance status within the group is a strong predictor of the use of scrounging tactics during social foraging (Barta & Giraldeau 1998; Dominoni 2017). In other systems, scrounging is found to be higher in females (Harten *et al.* 2018) or more socially central individuals (Aplin & Morand-Ferron 2017). These findings emphasise the importance of understanding social structure when addressing social foraging processes like the use of producer-scrounger strategies. The results from this thesis demonstrate that when sub-groups are highly flexible within a population, individual use of producing and scrounging strategies should also be flexible (**Chapter 4**) as has previously been shown in an experimental study of dynamic social group composition (Morand-Ferron *et al.* 2011).

Context dependent social foraging

Local enhancement is a common social foraging behaviour, that has been demonstrated to be of particular value in environments in which resources are patchily distributed (Pöysä 1992; Buckley 1997). The marine environment presents both persistent predictable features (Scales *et al.* 2014) as well as temporally and spatially variable features (Weimerskirch 2007). Previous research has demonstrated that higher environmental heterogeneity (patchiness), and persistent marine features such as oceanic fronts, concentrates marine resources in relatively high quality patches creating predictable hotspots that can result in higher concentration of foragers in these areas (Scales *et al.* 2014; Waggitt *et al.* 2018; Trevail *et al.* 2019). Thus, seabirds relying on more predictable environmental features may favour personal memory over social foraging information and therefore it is important to understand how social interactions differ in response to environmental features. In this thesis, I found that local enhancement occurred at a level above that expected by the spatial null model in gannets foraging in the Bass Strait only (**Chapter 3**) where individuals are known to forage on small schooling fish that present a less predictable resource (Wells *et al.* 2016). This demonstrates that that individuals adjust their foraging behaviours in response to the costs and benefits of forming social groups under different prey conditions. This finding is one of the first to establish the importance of context in social foraging decisions. An important extension to this

research would be to further assess how social foraging decisions are related to both persistent and temporal environmental features, particularly in relation to features known to influence prey type and distribution.

Understanding the location of prey patches in the ocean environment is difficult at the time-scale necessary to match seabird foraging movements to prey availability. The use of oceanographic features, such as chlorophyll concentration and water stratification are frequently used as a proxy to identify regions of high prey availability (i.e. Scott *et al.* 2010; Cox *et al.* 2016), and these environmental measures have been linked to prey abundance and encounter frequency (Hollowed *et al.* 2012; Waggitt *et al.* 2018). However, to date no studies of social foraging in seabirds have considered these environmental variables. In an ideal study system, simultaneous knowledge of the spatial distribution of both foraging seabirds and prey species would be needed to fully assess if social foraging behaviours allowed individuals to efficiently exploit available food patches. Through the use of sampling methods such as hydroacoustic surveys, it is possible to gain a highly detailed understanding of the real-time and fine-scale spatial movements of fish (i.e. Taylor *et al.* 2005; Hollowed *et al.* 2012; Muška *et al.* 2018). Although hydroacoustic survey methods have limitations in detecting fish along the surface (Trenkel *et al.* 2011) which limits the use of these surveys for some seabird species to which surface fish are the only available prey. Additionally, fish hydroacoustic surveys often focus only on commercially managed fish, or through opportunistic surveys, which vary in quality and require other complementary sampling to identify species level information (Trenkel *et al.* 2011). Therefore, concurrent data on fish movements and seabird foraging are rare and are currently only feasible on a very small scale (for example Waggitt *et al.* 2018). Future studies that are able to take advantage of increasing quantity of both seabird tracking and hydroacoustic sampling of fish movements would allow researchers to determine if foraging groups are accurately able to track available prey patches. Such work would be able to determine if seabirds are able to locate available prey patches through socially available information or if there is a mismatch in the location of foraging seabirds and the available prey distribution.

During the breeding season, seabird populations consume vast quantities of food (de L. Brooke 2004) and decreasing food availability and increased conflict with commercial fisheries has been found to be one of the key factors driving significant population declines observed across many seabird species (Bunce 2001; Croxall *et al.* 2012; Paleczny *et al.* 2015). These population declines may have a significant negative effect on the foraging success of individuals that rely on social information, due to the positive density dependence process, termed the Allee effect (Courchamp et al. 1999; Gil et al. 2018). During positive density dependence, social processes, such as social information use, become disrupted at densities below critical thresholds, which in turn can lead to population collapses (Courchamp et al. 1999; Gil et al. 2018). Such Allee effects have been documented previously in seabirds, with forager density significantly influencing foraging success (Grünbaum & Veit 2003). Therefore, understanding the individual and environmental drivers of social information use in seabird foraging in conjunction with either direct or indirect metrics of fish populations may be a vital component in the future study of seabird ecology.

Technological developments

With 85% of the breeding colony sampled, the work in this thesis presents the most comprehensive simultaneous sampling of social associations within a colonial species to date. However, even with this degree of coverage, the associations measured here represent a conservative measure of the total social associations by all individuals (**Chapter 2**), as untracked adults and juveniles would also be present in the population. The extensive coverage in this study limits the effects of such untracked individuals providing a robust minimum estimate for individual sociality, however future work assessing the associations with non-breeding individuals (i.e. juveniles) would be necessary to determine if these missed interactions are distributed evenly across individuals, or if certain classes or groups of individuals have different association rates with these missed individuals. The use of GPS devices avoids many of the concerns common to social networks including the risk of missed interactions and observation errors, such as mistaken identity or over-sampling of certain conspicuous individuals (James *et al.* 2009). The GPS sampling rate (two minutes) used in this thesis

provides a detailed look at the co-occurrences of individuals on a time scale that is relevant to foraging decisions in gannets while balancing the need for multi-trip recording. However while the behaviours studied in this thesis are determined from data with high spatial and temporal resolution, I was still unable to directly quantify the nature of the social association formed between individuals. As such, although this work provides strong evidence that individuals engage in exploitative following behaviours (**Chapter 4**) individuals could also benefit from group travel if commuting in groups decreases search time (e.g. Bijleveld *et al.* 2015), decreases movement costs (e.g. Weimerskirch *et al.* 2001; Portugal *et al.* 2014), or if groups of foragers are more efficient at exploiting resources (e.g. Brown *et al.* 1991; McInnes *et al.* 2017). Direct observations of interactions or a higher sampling resolution is necessary to fully study the coordination of group flight behaviours. For example, extremely high resolution GPS devices that measure position at a rate of once a second or higher, can allow researchers to identify direct copying of other individuals movement choices. Such fine-scale movement analysis has been successfully used to assess following behaviours in coordinated group movements in homing pigeon (*Columba livia domestica*) and white storks (*Ciconia ciconia*) (Nagy *et al.* 2010, 2018).

Conclusions

Throughout this thesis, I provide evidence of the importance of social foraging associations to colonially breeding seabirds. I demonstrate that local enhancement may be a key social foraging behaviour, particularly in environments dominated by patchy prey resources such as small shoaling fish. Additionally, my work builds on that from many other social systems to emphasise that even in densely aggregated colonial systems, individuals express variability in their sociality and foraging decisions. This provides further evidence that addressing individual variability may be an important consideration when studying population level processes.

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